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Interaction entre la mémoire de travail et l'attention sélective dans le domaine auditif non-verbal

Salomé Blain

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Interaction of non-verbal auditory selective attention and working memory

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Abstract

The work of this thesis aims to clarify the interaction between selective attention and working memory. This interaction has been studied mainly in the visual domain, or focused in the auditory domain on verbal stimuli, and during the stages of memory retention or access to the retained information. Here, we design a paradigm to study this interaction using non-verbal auditory stimuli (musical stimuli) during the encoding step of working memory.

This paradigm has been behaviorally tested on different groups of participants: non-musicians, professional musicians, people with low or high frequency of dream recall at awakening. The associated results led to the understanding that working memory and selective attention call for common cognitive resources, and that when the working memory task calls for greater resources, the difficulty of inhibiting distractors is amplified. We found that musicians, with better working memory capabilities, were at an advantage for higher memory loads, under which they could better inhibit distracting sounds. We also showed that low frequency dream recallers tended to respond less quickly but more accurately than high frequency dream recallers, revealing greater resistance to auditory distractors. Finally, we assessed the cerebral basis of auditory attention and memory interaction using this new paradigm with magnetoencephalography. The first results highlight the impact of selective attention on sustained evoked responses and on late latency evoked potentials, but the interaction observed at the behavioral level has not yet been observed at the level of neural correlates.

Finally, this work lays the foundations for further investigations, at the cerebral level but also for a future characterization of the evolution of this interaction between attention and memory during childhood, which has not yet been described. A better understanding of this interaction may enable better management of people with memory deficits (brain lesions, for example) or attention deficits (ADHD children in particular), by implementing more appropriate behavioral therapies. Indeed, by taking into account the sharing of resources between selective attention and working memory, we can hope to find remedies that will allow resources to be better distributed towards one or other of the processes.

Keywords:

Cognition, Psychology, Selective attention, Working Memory, Short-Term Memory, Auditory Perception, Dichotic Listening, Delayed Matching-to-Sample, Non-verbal, Music, Behavior, MEG.

Résumé

Le travail de cette thèse vise à comprendre l'interaction entre l'attention sélective et la mémoire de travail. Cette interaction a été principalement étudiée dans le domaine visuel, et s'est focalisée dans le domaine auditif sur des stimuli verbaux, et ce, pendant les étapes de rétention mnésique ou d'accès à l'information retenue. Ici, nous avons développé un paradigme permettant d'étudier cette interaction à l'aide de stimuli auditifs non verbaux (stimuli musicaux), et ce pendant l'encodage en mémoire de travail.

Ce paradigme a été testé au niveau comportemental sur différents groupes de participants : des non-musicien·ne·s, musicien·ne·s professionnel·le·s, des personnes se souvenant peu ou beaucoup de leurs rêves au réveil. Les résultats ont permis de montrer que mémoire de travail et attention sélective faisaient appel à des ressources cognitives communes, et que lorsque la tâche de mémoire de travail sollicite de plus importantes ressources, la difficulté d'inhibition des distracteurs est amplifiée. Nous avons mis en évidence que les musicien·ne·s, grâce à de meilleures capacités de mémoire de travail, étaient avantagés pour de plus hautes charges mnésiques, sous lesquelles iels pouvaient mieux inhiber des sons distracteurs. Nous avons également montré que les petits rêveurs avaient tendance à répondre moins rapidement mais plus justement que les grands rêveurs, révélant une plus grande résistance aux sons distracteurs. Enfin, nous avons évalué les bases cérébrales de l'interaction entre l'attention auditive et la mémoire en combinant ce nouveau paradigme avec des enregistrements en magnéto-encéphalographie. Les premiers résultats permettent de mettre en évidence l'impact de l'attention sélective sur la réponse évoquée lente et sur les potentiels évoqués de latence tardive, mais l'interaction observée au niveau comportemental n'a pas encore été observée au niveau des corrélats neuronaux.

Finalement, ce travail pose les bases d'investigations futures, au niveau cérébral mais aussi pour une caractérisation de l'évolution de cette interaction entre attention et mémoire au cours de l'enfance, qui n'a pas encore été décrite à ce jour. Une meilleure compréhension de cette interaction peut permettre de mieux prendre en charge des personnes présentant des déficits mnésiques (lésions cérébrales, par exemple) ou des déficits attentionnels (enfants TDAH en particulier), en mettant en place des thérapies comportementales plus adaptées. En effet, en prenant en compte le partage de ressources de l'attention et de la mémoire de travail, on peut espérer trouver des remédiations permettant de mieux répartir les ressources vers l'un ou l'autre des processus.

Mots-clefs :

Cognition, Psychologie, Attention Sélective, Mémoire de Travail, Mémoire à Court Terme, Perception Auditive, Écoute Dichotique, Appariement Différé, Non-verbal, Musique, Comportement, MEG.

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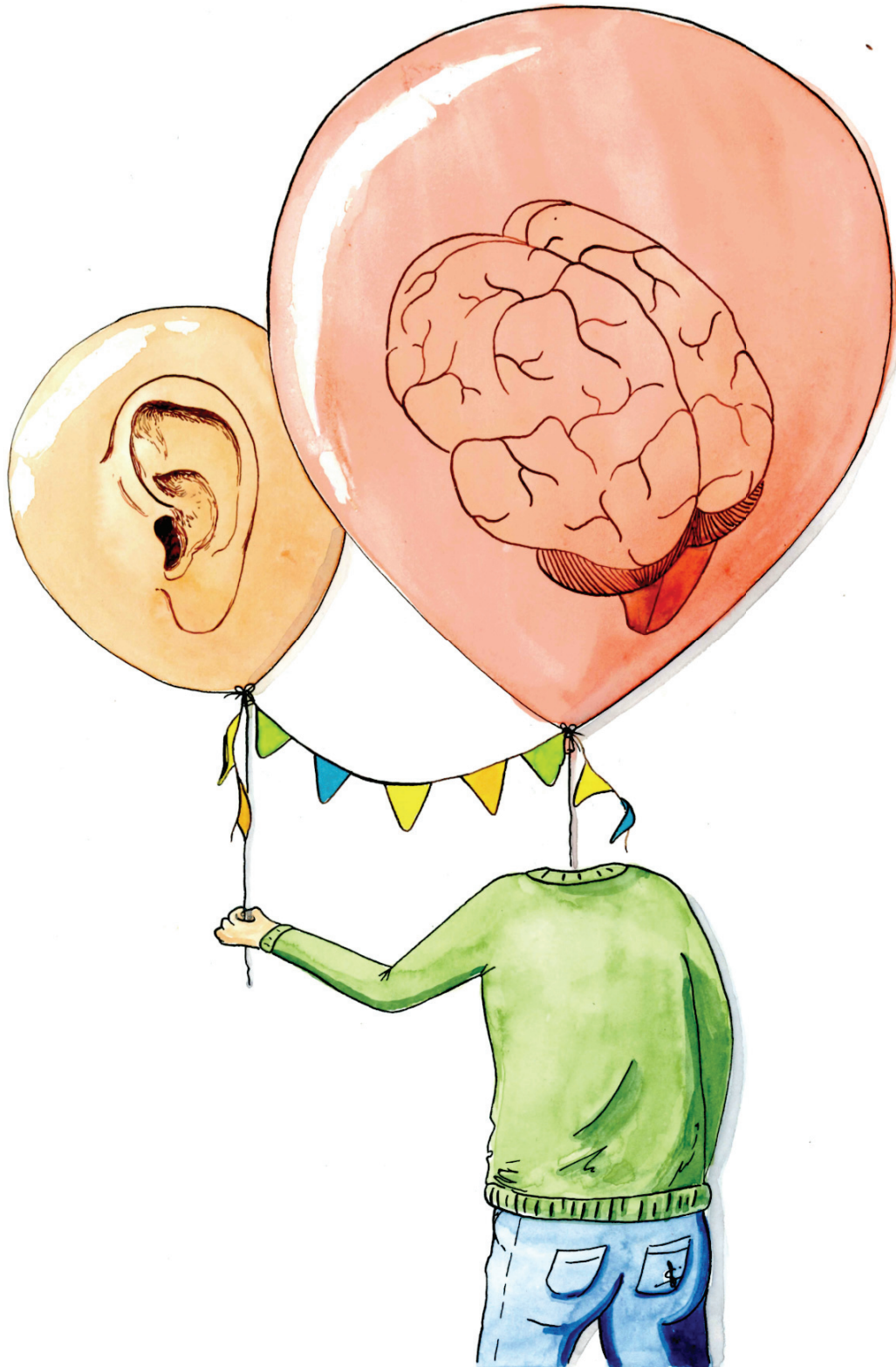
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I. Introduction



AUDITORY PERCEPTION AND COGNITION

Every human being experiences the surrounding world through his/her senses: every environmental information is translated to an inner perception thanks to the multiplicity of perceptual (or sensorial) systems (olfactory, gustatory, somatosensory, visual, and auditory). The access to the translated information might not be always present, but both conscious and unconscious perceptions require sensory information to be processed by the perceptual system. Physiology, cognitive psychology, and neuroscience have tried to investigate how the sound is translated and integrated in the ear, then in the brain.

A) Anatomy of the auditory system

Sounds result from a series of rhythmic compressions and rarefactions of the air, which can be described as a sinusoid characterized by its amplitude and period (or frequency). Complex natural sounds are a combination of different sinusoids with different parameters, which enter through the pinna (also called auricle, see Figure 1) to the auditory canal.

1) *Anatomy of the ear*

The ear is divided in three main parts: outer ear, middle ear, and inner ear (see Figure 1). The outer ear focuses sound waves into the ear canal and amplifies medium sound frequencies (1500-7000Hz). In the middle ear, small bones called ossicles transmit sound energy from the eardrum to the oval window in the inner ear. The inner ear is composed of a complex structure, partly spiralis, partly tubular, called the cochlea. In this structure, an electro-mechanical transduction is performed by the hair cells. The human cochlea counts 12.000 outer hair cells and 3.500 inner hair cells and is organized in a tonotopic fashion along the basilar membrane: for each frequency, the vibration of the basilar membrane is located to a dedicated place. This frequency selectivity is due to passive mechanisms (mechanical properties of the cochlea) and active mechanisms (cellular activity of the outer hair cells).

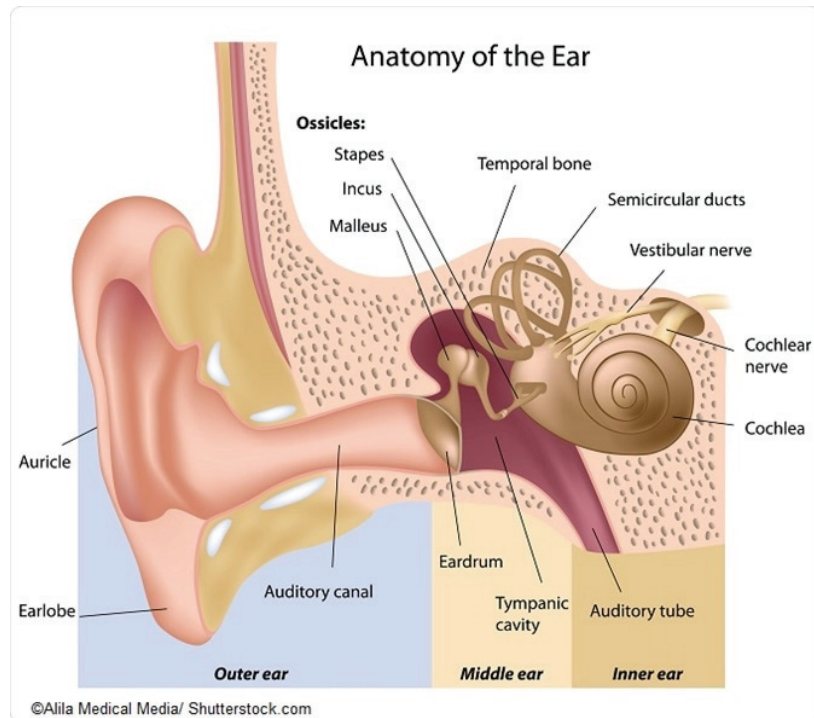


Figure 1 - Diagram of the ear anatomy.

2) *From the ear to the brain: auditory pathways*

The vibration of the basilar membrane is translated into a neural signal in the organ of Corti, at the center of the cochlea. The signal is then transmitted to the auditory nerve, in which the timing structure of the acoustic stimulus is encoded. This signal corresponds to a mixture of the different sound sources, analyzed according to frequency bands. The tonotopic organization of the cochlea is preserved in the auditory nerve, as each fiber corresponds to a specific frequency.

The information coming from both ears is redirected into sub-cortical structures: the cochlear nuclei, the superior olive, the lateral lemniscus, the inferior colliculus, and finally the thalamus (see Figure 2): the cochlear nuclei are divided in two parts, the ventral side where the responses correspond to the ones of the auditory nerve, and the dorsal side where more complex responses emerge. The ventral neurons project ipsi- and contra- laterally on the superior olive, in which the position of the stimuli is evaluated. Dorsal neurons of the cochlear nuclei and superior olive neurons project on the lateral lemniscus and then to the colliculus. Two pathways begin in the colliculus: the first one is tonotopic and reaches the thalamus and then the primary auditory cortex; the other one is diffuse and multisensory, reaching first the thalamus and then the auditory associative areas.

3) Auditory cortex

The auditory cortex is located in the superior temporal lobe, deep into the Sylvian sulcus, and extend to the superior temporal gyrus and surrounding parietal and insular cortices. It is composed of a primary auditory cortex and of associative auditory areas. Several areas present a tonotopic organization, just like the pathways from the cochlea (see Figure 3).

The different portions of the auditory cortex have different functional roles in the integration of auditory stimuli. For example, the primary auditory cortex is preferentially activated by pure sounds, whereas the associative areas are more sensitive to complex sounds (Wessinger et al., 2001).

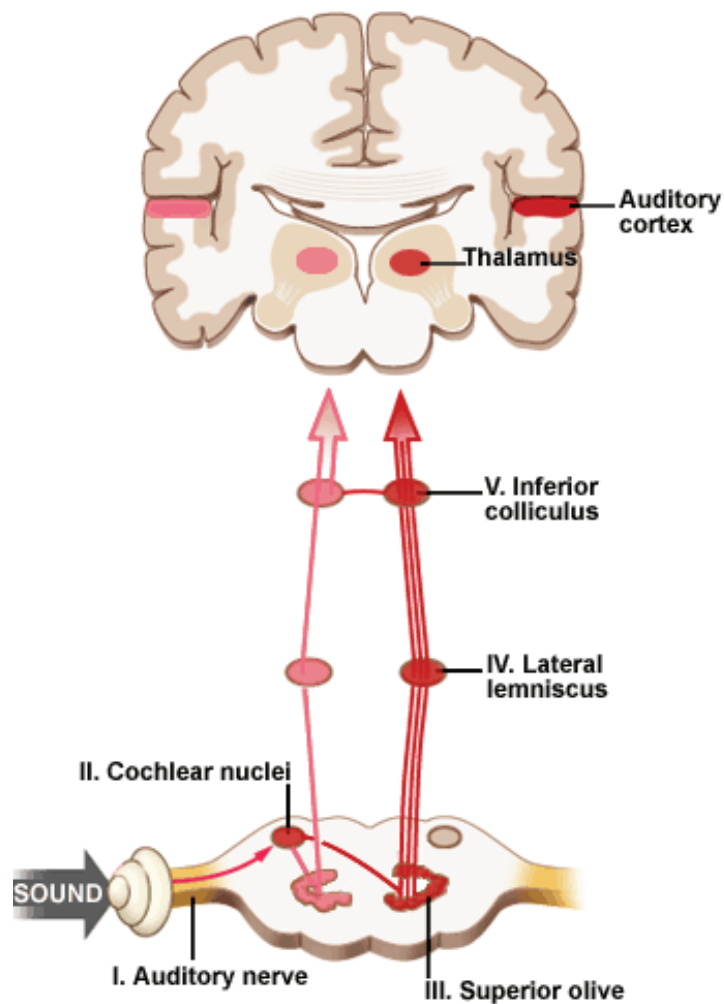


Figure 2 - The human auditory pathway, from the cochlea to the auditory cortex (from Stéphan Blatrix)

4) Other associative areas

In the visual modality, it has been shown that the processing of a visual stimulus recruits not only the visual cortex, but also involves frontal areas (Mishkin et al., 1983). Similarly, two main pathways have been distinguished in the auditory domain: one projects from the anterior auditory areas to the ventral prefrontal cortex and is linked with the processing of the sound content (marked in red in Figure 3), the other projects from the posterior auditory cortex to the dorso-lateral prefrontal cortex (marked in blue in Figure 3) and is linked with the spatial information of the stimulus (Kaas & Hackett, 1999; Rauschecker, 1998).

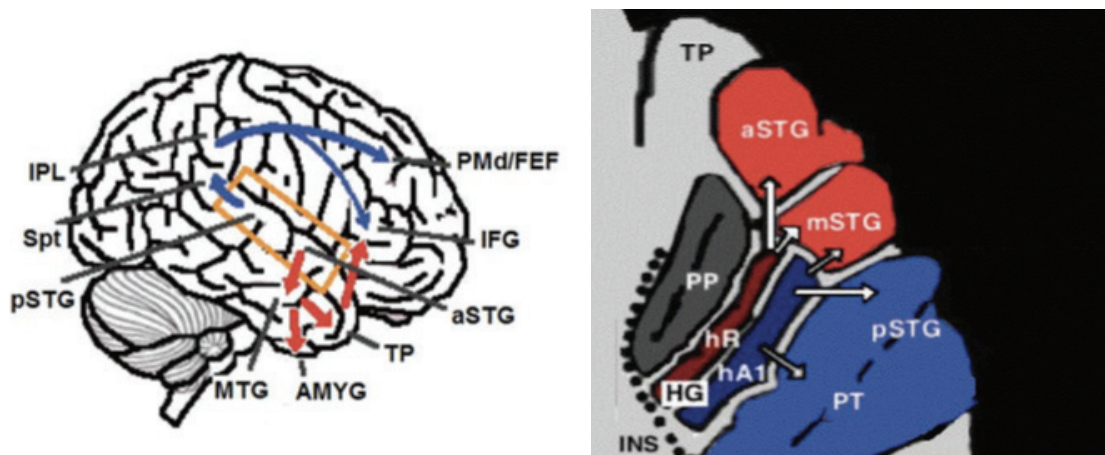


Figure 3 - Dual stream connectivity between the auditory cortex and frontal lobe in humans.
Left: the human brain is schematically depicted and displayed from the side. The orange frame marks the region of the auditory cortex. Blue colors mark pathways affiliated with the Auditory Dorsal Stream (ADS), and red colors mark pathways affiliated with the Auditory Ventral Stream (AVS).
Right: the human auditory cortex is schematically depicted on the supratemporal plane and observed from above, with the parieto-frontal operculum removed. Arrows represent the connectivity measured between the different areas. Dark red and blue regions mark the primary auditory fields.
Abbreviations: AMYG – amygdala, HG-Heschl’s gyrus (with hR and hA1 areas R and A1), FEF – frontal eye field, IFG – inferior frontal gyrus, INS – insula, IPL – intra-parietal lobule, MTG – middle temporal gyrus, PMd – dorsal premotor cortex, PP – planum polare, PT – planum temporale, TP – temporal Pole, Spt – Sylvian parietal-temporal, pSTG/mSTG/aSTG – posterior/middle/anterior superior temporal gyrus, (adapted from Poliva, 2017).

From the ear to the brain, we described above the anatomical pathway for sound information transmission. In everyday life, the auditory environment is composed of multiple sound sources, and each of these sources has its own time course. We often automatically extract one or several of these sources, depending on the context, maybe in order to use one piece of information later on. This leads us to question how these processes are operated: how do we segregate different environmental sources (auditory scene analysis)? How do we select one relevant versus other irrelevant streams of sounds (selective/divided attention)? How do we memorize auditory information?

B) Psychology of hearing

Experimental psychology aims to characterize human mental faculties thanks to behavioral methods. Psychology of hearing can be divided into three main fields: 1) psychoacoustics, which analyzes the relationship between the sensation of hearing and the physical characteristics of the stimulus, 2) cognitive psychology of audition, which tries to decompose auditory perception into smaller interacting processes, and 3) neuropsychology of hearing, which focuses on the behavioral effects of brain damage in patients, bridging psychology and neurology. These three main fields have prospected the different aspects of auditory perception. We will present briefly the associated main results, in particular coming from cognitive psychology.

1) Auditory scene analysis

Auditory scene analysis is the process thanks to which one can decompose a given sound mixture in several streams of sounds. It has been shown to rely on two main mechanisms: primitive scene analysis and schema-driven analysis (Bregman, 1994). Primitive scene analysis is a probably automatic and innate process based on the features of incoming acoustic data. The continuity principle (emission and disturbance rarely coincide between two sources, volume changes are likely to be continuous, changes are likely to impact all components of a same sound) and complexity principle (vibrating objects often emit harmonic sounds) allow to distinguish several sound sources. Schema-driven analysis is an acquired process constraining auditory representation construction according to the listener's previously acquired knowledge on familiar patterns or schemas of the acoustic environment.

Auditory scene analysis is completed by the capacity to recognize sound sources. Recognition of sound sources is a complex problem: it consists in distinguishing each auditory stream from a whole range of other sounds (Wood & Cowan, 1995). Interestingly, thanks to the extraction of auditory attributes, one can indeed distinguish different individuals thanks to their voices. In a way, source recognition is a sub-process of sound properties extraction (McAdams, 1993). A sound produced by one object can vary from one moment to another one, depending on the context; therefore, it is necessary to extract acoustic invariants in order to overcome this contextual effect (McAdams, 1993). This is why source recognition relies on the listener's use of previously acquired knowledge and on the information stored in memory.

The use of prior knowledge to extract sound information has been described as the “descending” pathway of sound perception. It can influence sound perception in many ways. For example, a given melody is easier to recognize in a distracting sound background if it has been listened (and memorized) earlier (Bey & McAdams, 2003; Jay Dowling et al., 1987). Thanks to electrophysiological studies, it has been shown that attention variation can impact this descending pathway: attention focus changes the organization of attended (Sussman et al., 1998) and unattended (Sussman et al., 2005) sounds.

2) *Auditory traces*

An auditory trace is a brain representation of auditory information. Auditory traces can be stored for various durations, which gives birth to the definition of different sub-types of memory processing: echoic memory, short-term memory, and long-term memory.

Echoic memory is an early sensory store that can be used in stimulus recognition. It is composed of two sub-stores, one lasting 150 to 300 milliseconds, and another one lasting until 10s (for a review, see Cowan, 1984). In practice, it can be viewed as a buffer in which the traces are automatically generated than a memory store with voluntary action on what is memorized. Short-term memory is a process allowing to retain actively auditory information through a limited time and is discussed in depth in the second chapter – AUDITORY NON-VERBAL WORKING MEMORY. Auditory long-term memory allows the retention of auditory information over long periods of time (minutes to years), and in particular the recognition of familiar sounds.

3) *Auditory attention*

Attention can be defined as the process allowing to perform the selection of a given sensory information (see the third chapter – AUDITORY SELECTIVE ATTENTION). Therefore, the number of items and the nature of the accessible auditory information can be impacted by attention (Awh et al., 2000; Awh & Jonides, 2001; Fougne, 2008; Gazzaley, 2011; Dowling, 2012; Rutman et al., 2009; Theeuwes et al., 2011).

4) *Pitch perception*

As described above, a sound is characterized by several dimensions/features (frequency, intensity, duration, position) giving birth to several auditory attributes (pitch, loudness, duration, timbre, localization). Pitch is related to frequency and has raised many interrogations and interest. The pitch of a note indicates how low or high the note is (ANSI, 1973). It can also be defined as the quality of the sound governed by the rate of vibrations producing it. Pitch perception is essential for many auditory processes: sound source segregation and recognition, for example, but also for understanding prosody (emotions and intentions conveyed by speech thanks to pitch variations). It is also a key component of music comprehension and harmony.

Pitch perception is a major sub-component of music perception. An influential model explaining music perception relies on a pitch organization module and a time organization module (Peretz & Coltheart, 2003). This model is based partly on brain lesion studies in which brain damage results in impaired pitch perception and not rhythm perception, and vice-versa. The pitch organization module is itself based on two subcomponents: the interval code that contain the pitch changes between notes (Dowling, 1982) and the contour, *i.e.* the pattern of ups and downs.

Pitch perception has been shown to be sensitive to context, at least in memory tasks: when participants are required to discriminate the pitch of two sounds presented at the beginning and at the end of a three-sounds-long sequence, the middle sound could disturb performances. The effect is more important when pitch of the distractors is similar to the pitch of the targets (Deutsch, 1970). Pitch is also submitted to the musical knowledge context, therefore related to long-term memory: knowledge of the western construct of scales impact pitch perception (Bigand et al., 2007; Marmel et al., 2008; Warrier & Zatorre, 2002).

C) Neurophysiological aspects of auditory perception

1) *Access to auditory brain function*

Brain activity is derived from every single cell activation: a neuron receiving information from other neurons via synaptic communication upon its dendrites transfers a new message to its target neurons through its axon. The processing of information is allowed by the coordination of populations of neurons. Several methods in cognitive neuroscience were elaborated to explore brain functioning, they are briefly described in the following paragraphs.

a. Single unit electrophysiology

Single- and multi- unit electrophysiology focuses on the electrical recordings of cell activity. It is used in animals, with use of electrodes that are implanted in a given cerebral region of interest. It also allows to record the activity of a population of cells, by measuring the local field potential that reflects post-synaptic activities.

b. Human electrophysiology

Local recordings are also possible in humans, in specific cases. Indeed, in case of pharmaco-resistant epilepsy, patients sometimes benefit of the implantation of intra-cerebral electrodes for clinical investigation before surgery. Recording is possible during the realization of perceptual or cognitive tasks.

Non-invasive recordings are also possible thanks to different approaches and sensors. The most used methods are electroencephalography (EEG) and magnetoencephalography (MEG) which measure electrical potentials and magnetic fields in the brain respectively, via sensors disposed on the scalp or close to the scalp. When neurons with a similar orientation coordinately release neurotransmitters, their activity is very similar to the one of a current dipole and a large signal can be recorded on the scalp. This signal is a reflection of a distant post-synaptic activity and can be recorded with fine temporal resolution (milliseconds). With EEG, spatial resolution is less optimal compared to MEG, and a source reconstruction of the generators is a complex problem. MEG is less impacted than EEG by anisotropy variations of the brain tissues (Güllmar et al., 2010). For auditory-related activity in particular, MEG greater sensitivity to the temporal lobe activity might be of great help (Alho, 1995). However, as the magnetic field is attenuated more rapidly than electric signal with distance, MEG is less sensitive to deep sources than EEG.

c. Metabolic cerebral imaging

Several methods are based on biological parameters indicating the metabolic activity of each area in the brain: PET, MRI, and NIRS.

Positron Emission Topography (PET) measures the local concentration of a radioactive marker, which can be either H₂O or glucose, in order to estimate the blood flow or local consumption of glucose. Functional Magnetic Resonance Imaging (fMRI) also measures changes in blood flow. A strong magnetic field is applied, which changes the orientation of the spins of the atoms of oxygen. The re-alignment of atoms indicates the blood oxygen level as well as the changes in blood flow (BOLD imaging: blood oxygen level dependent). PET and MRI have high spatial resolution (mm), but low time resolution: the time to acquire measures for the entire brain is long (2s for fMRI) and the measured metabolic changes are slow and occur relatively late after stimulation (several seconds).

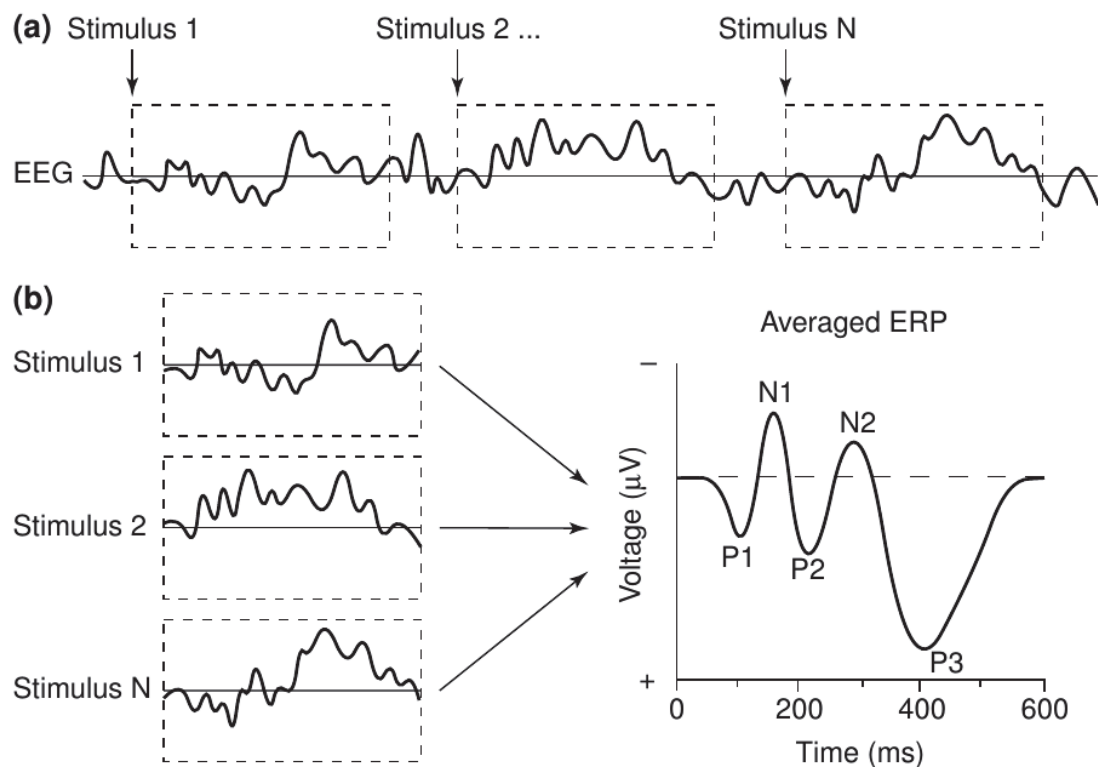
One other recent method is functional Near-InfraRed Spectroscopy (fNIRS). This method is based on the fact that optical properties of a tissue is influenced by its functional state. Skin, tissue, and bone are mostly transparent to NIR whereas hemoglobin and deoxygenated hemoglobin absorb lights: differences in the absorption spectra of deoxy-hemoglobin and oxy-hemoglobin allow the measurement of relative changes in hemoglobin concentration. This technique does not allow to measure reliably deeper brain structures and is very well adapted for babies or young children. Its spatial resolution on superficial structures goes from 1-2cm to 5mm. It has a temporal resolution of approximatively 0.1s; however, the measured changes are slow and occur, as for fMRI, relatively late after stimulation (seconds).

2) *Electrophysiological correlates of auditory perception*

Original concepts in neuroscience have associated perceptual systems with different isolated areas. However, recent theories do not restrict themselves to these areas, but tend to explain that perception is supported by highly hierarchically organized functional systems involving dynamic interactions between several brain areas. The brain would be a computational system, designed to interpret and make inferences about properties of a physical environment (Friston, 2003). In the present PhD thesis, we will consider that perceptual (auditory) processing is supported by local- and large- scale interactions between several brain areas, containing classical auditory pathways and prefrontal areas, as explained above (see *Other associative areas*).

a. Auditory evoked potentials

From MEG and EEG are extracted time series of magnetic field / potential variations, reflecting the activity of several cerebral generators. One of the ways to analyze these data is to isolate a time window around the stimulus presentation, across trials, and to compute the mean of activation for each time point across trials (see Figure 4). This method needs a high number of repetitions of the stimulus and allows noise reduction resulting from spontaneous brain activity, whose phase to the stimulus is random.



trends in Cognitive Sciences

Figure 4 - Illustration of the evoked potentials method (from Luck et al., 2000)

For each sensor, the result of the computation is a series across time of deflections, positive or negative, called event related potentials (ERP) in EEG, or event related fields (ERF) in MEG. Each potential or field is characterized by its latency and sign (positive or negative), but also its topography, *i.e.*, its distribution on the human scalp. Auditory evoked potentials have been mostly studied through scalp non-invasive EEG and are classified in three groups: early, middle, and late latency auditory EP (see Figure 5). In the following explanations, we will talk about ER (Evoked Response), referring to both ERPs and ERFs.

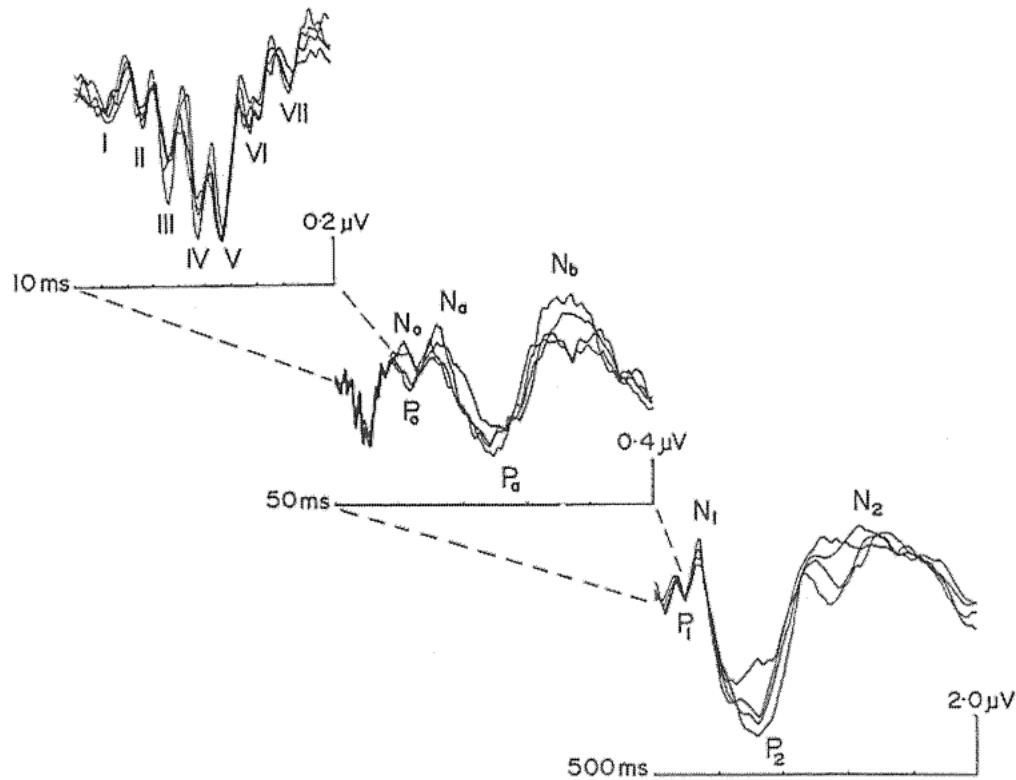


Figure 5 - Auditory evoked potentials. Positivity is down. The three panels correspond to early, middle and late latency auditory evoked potentials (from the left to the right) (Picton & Stuss, 1980)

Early latency ER happen in the 10 to 12 milliseconds after the stimulus presentation and are seven small signal deflections reflecting the activity in the auditory nerve and the income of auditory information in the sub-cortical structures.

Middle latency ER happen between 10 to 50 ms post-stimulus and are more variable across individuals. They are generated in the superior temporal cortex: the arrival of auditory information in the auditory cortex could happen from 12 to 14ms after the stimulus presentation (Liégeois-Chauvel et al., 1994; Yvert et al., 2005).

Late latency ER happen from 50 to 500ms after the stimulus presentation. The first positive ER is the P₅₀, which is followed by the negative N₁₀₀ and positive P₂₀₀. P₅₀, N₁₀₀ and P₂₀₀ considered as obligatory auditory potentials, which means that they reflect the minimal treatment by the auditory system, which can happen even when attention is not directed towards the stimulus or the auditory modality. Another late latency ER is the negative N₂₀₀, which can be observed if the sound is played for a longer period of time.

Intracranial recordings showed that the late latency potential P₅₀ is generated within the primary auditory cortex (Pantev et al., 1995; Yvert et al., 2002). EEG and MEG combination allow to better understand brain activation: they show an association of P₅₀ with the posterior supratemporal gyrus, the superior temporal and frontal gyri, the inferior temporal and frontal gyri, the posterior central gyrus, and the intraparietal sulcus, Heschl's gyrus, orbito-parietal regions and the right temporo-parietal junction (Edgar et al., 2003; Korzyukov et al., 2007; Lecaigard et al., 2019; Mäkelä et al., 1994; Weisser et al., 2001).

N₁₀₀ (or N1) is composed of different subcomponents. First, there is first a fronto-central negativity, peaking at 100ms and generated in the auditory cortex (superior temporal lobe) and in the frontal area (Alcaini et al., 1994; Giard et al., 1994). The second component is generated in the temporal superior gyrus, which can be observed on temporal electrodes as a positive wave at 100ms and a negative one at 150ms (Näätänen & Picton, 1987). A third central negative component seems to be elicited only for low frequency presentation stimuli and might be related to the reorienting of attention after an infrequent stimulus.

The N1 has been shown to be generated in several areas of the auditory cortex (Liégeois-Chauvel et al., 1994; Yvert et al., 2005). Its generators show a tonotopic organization (Bertrand et al., 1991; Pantev et al., 1995; Verkindt et al., 1995). As the temporal component of the N1 has also been observed after rapid and important acoustic changes, it is supposed to be associated with detection of the beginning of sounds or acoustic transients (Hari & Mäkelä, 1988; Näätänen, 1990; Näätänen & Winkler, 1999). Its amplitude correlates with detection threshold but not with pitch variation detection, which implies that it does not totally overlap with physical properties recognition. Finally, it has been proposed that auditory processing rests on a spatial progression within the supratemporal area, starting from posterior (at N1 latency) to anterior areas (Maess et al., 2007; Näätänen & Alho, 1995; Recasens et al., 2014; Rosburg et al., 2004).

Late latency potentials can be reduced over repetitions, which can be explained by refractoriness or neuronal adaptation concepts. Refractoriness refers to the period of time required for a neuron to fire following a first activation, whereas neuronal adaptation refers to more long-term changes in the receptive field of a neuron after the repetition of a stimulus (Perez-Gonzalez & Malmierca, 2014). The N1 has been shown to be very sensitive to sound repetitions. If impacted by refractoriness processes, this sensitivity could imply a decrease in amplitude stabilized rapidly towards a floor effect, whereas an impact of neuronal adaptation

could imply a continuous and potentially infinite decrease or change of the amplitude. As shown by Demarquay and colleagues (2011), the N1 amplitude decreases during the presentation of 2 to 3 tones and acquires then a stabilization value: N1 amplitude decrease could be attributed to refractoriness.

Sustained ERs are slow responses lasting as long as the stimulation does. They have not been extensively studied in the auditory domain. However, a few studies showed that sustained evoked responses are involved in the cortical representation of behaviorally relevant sounds (Bidet-Caulet et al., 2007; Picton et al., 1978) and are modulated by attentional processes (Picton et al., 1978). The topographies of sustained evoked responses in secondary auditory areas for long-lasting stimuli are bilateral (Albouy et al., 2013; Bidet-Caulet et al., 2007). In MEG, higher amplitude is observed in temporal compared to frontal sensors; higher amplitude is observed in the left compared to the right hemisphere for musical tones (Albouy et al., 2013).

b. Oscillatory responses to auditory stimulation

(i) Measurement of oscillatory responses

In response to sound stimulation, another type of brain response can be recorded using electrophysiology: oscillatory activity. Oscillation analysis is based in the decomposition of the signal thanks to a convolution method with a family of wavelets. This convolution creates a time-frequency profile of the signal power for each trial. It is then possible to compute the average of each response to the stimulus in order to estimate the oscillatory activities associated across trials. Oscillations are observed in different frequency bands, from delta (<4Hz) and theta (4.5-8Hz) to alpha (8.5-12Hz), beta (12-30Hz), and gamma (>30Hz).

There are three types of oscillations: evoked, induced, or steady state. Evoked and induced refer to what is associated with the presence of a stimulus, whereas steady state is elicited to periodically modulated stimulus (Bertrand & Tallon-Baudry, 2000; Tallon-Baudry & Bertrand, 1999). If we take the gamma band (>30Hz) as an example: the difference between evoked and induced gamma rely on their phase-locking to the stimulus: evoked gamma is precisely time-locked to the stimulus (see Figure 6 - A. and C.) whereas the temporal association of induced gamma (see Figure 6 - A., B. and D.) with stimulus onset is rather loose (Bertrand & Tallon-Baudry, 2000; Tallon-Baudry & Bertrand, 1999).

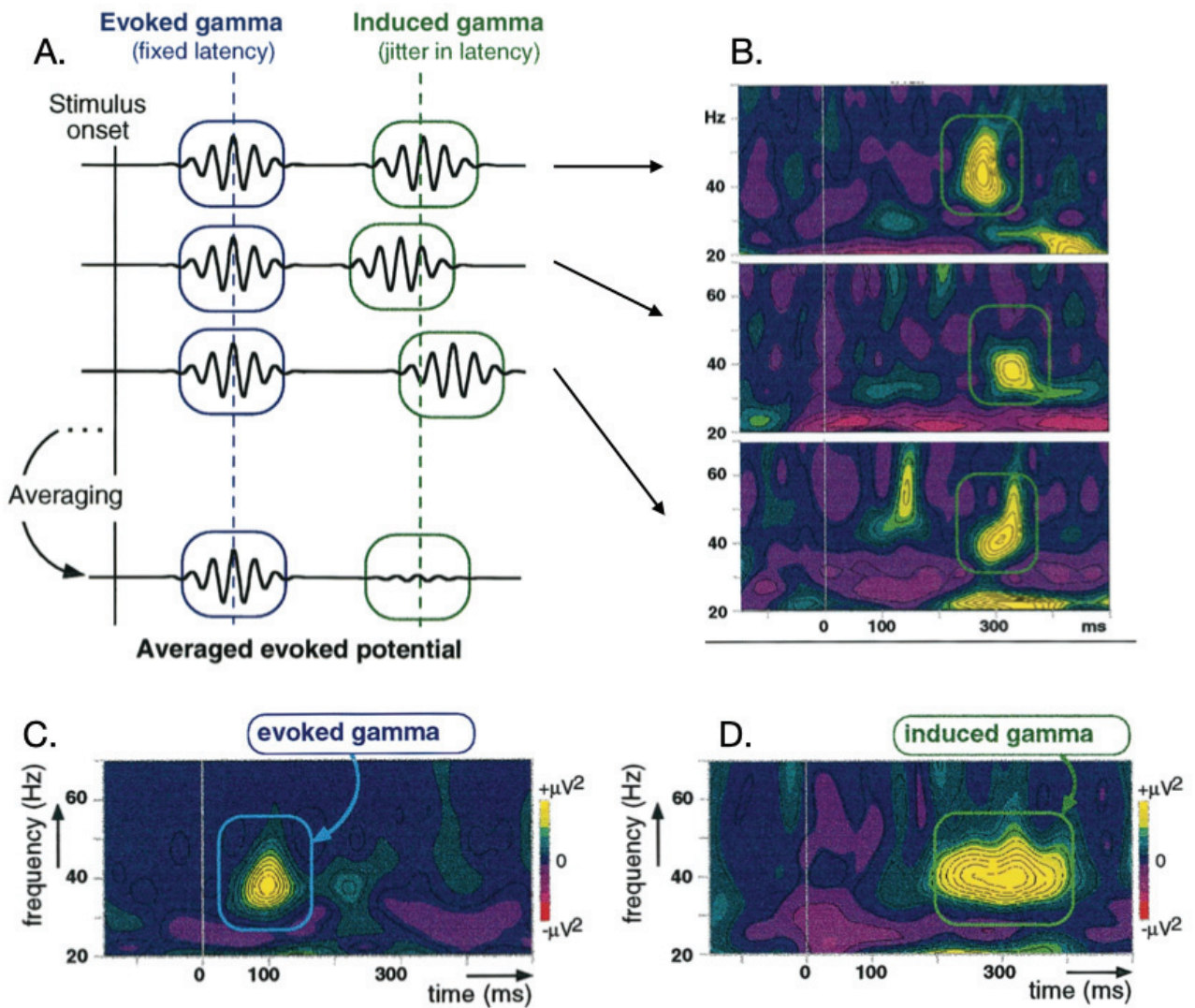


Figure 6 – Evoked and induced gamma oscillation response. *A.* An evoked response (blue boxes) appears at the same latency and phase in each single trial and hence can be detected in the averaged evoked potential. An induced response (green boxes) appears with a jitter in latency from one trial to another, centered around a given latency (green line). It therefore tends to cancel out completely in the averaged evoked potential. *C.* Time-frequency power representation of the average across trials, the power is computed after averaging. *B.* To study induced gamma, one must first compute the time-frequency power for each trial, as represented here. It can then be averaged across trials, as represented in *D.* (adapted from Tallon-Baudry, 1999)

(ii) Different oscillatory responses to auditory perception

It has been shown that 40Hz oscillations are associated with perceptual integration (Lachaux et al., 2005; Tallon-Baudry et al., 1999). Gamma oscillations (30-40Hz) was first considered as noise, but its importance in perception was rapidly brought to light (for a review, see Rieder et al., 2011). Oscillatory activities superior to 30 Hz might be involved in several high-cognitive processes such as learning (Gruber et al., 2004; Miltner et al., 1999), memory (Gruber et al., 2004; Sederberg et al., 2003; Summerfield & Mangels, 2005; Tallon-Baudry et al., 1999; Vidal et al., 2006), attention (Tallon-Baudry et al., 2005; Vidal et al., 2006), or target detection (Gurtubay et al., 2004).

Connectivity analyses on power-to-power, phase-to-power, or phase-to-phase interactions allow to dig into interactions between frequencies or between areas. When listening to speech, a decrease of communication is observed via high frequencies (>70Hz) from the primary auditory cortex (PAC) to the anterior cingulate cortex (ACC), whereas there is an increase of communication from the ACC to the PAC via low-frequencies (<30Hz) (Arnal & Giraud, 2012; Bosman et al., 2012; Fontolan et al., 2014; Panzeri et al., 2010; Sauseng et al., 2008; Walker et al., 2011), reflecting that endogenous and exogenous information circulate through different frequency channels. Gamma is interpreted as an index of the communication between brain regions: coherence between two pools of cells would allow information transfer (Fries, 2005).

The alpha oscillatory band (5-15Hz) has also been shown to be involved in primary sensory auditory processing (Başar & Schürmann, 1994; Schürmann et al., 1997). Alpha rhythm has been discovered by Hans Berger (1929): this 5 to 15Hz oscillation appears when the eyes of the participant are closed. It was first associated with a reduced cortical brain activity (Pfurtscheller et al., 1996) but appeared later to be related to neurons excitability. The main hypothesis of alpha role in brain functioning was the theory of the timing inhibition (Klimesch et al., 2007). According to this theory, the alpha rhythm would be generated by the firing rate of inhibition cells: an increased firing of the inhibitory cells would imply inhibition of the associated brain area, whereas a decrease would imply a decrease of inhibition. The synchronized action of inhibitory cells, as revealed by the power of the alpha oscillation, reflects then directly the state of activity of the area: an increase in alpha power (synchronization) implies a reduced activity, a decrease in alpha power (desynchronization) implies an enhanced activity.

Most of the experimental results confirms this theory; however, please note that opposite ideas has also been proposed: according to Palva and Palva, there is a discrepancy between the assigned inhibitory role of alpha oscillations and evidence of increases in alpha power in frontal and parietal regions, which are task-relevant regions. According to them, higher alpha phase synchronization indexes increased internal information processing (Palva & Palva, 2011).

Alpha rhythm was mainly studied in the visual domain, as a continuity of Hans Berger's work, but not only (Berger, 1929). Several technical limitations prevent from studying alpha in the auditory modality. In the first place, the organization of the auditory cortex itself does not allow a simple access to alpha rhythm. Indeed, the orientation of the cortex generators prevents EEG from revealing such rhythm (Weisz et al., 2011). Furthermore, its reduced size and its proximity with the motor cortex creates doubts about its origin. However, thanks to MEG recordings and source reconstruction, it is now admitted that alpha rhythm can be generated by the auditory cortex (see Figure 7), as it was first revealed by Weisz and Muller (2014) and then replicated through several experiments (ElShafei et al., 2018; Frey et al., 2015; Weise, 2016; Weisz & Obleser, 2014).

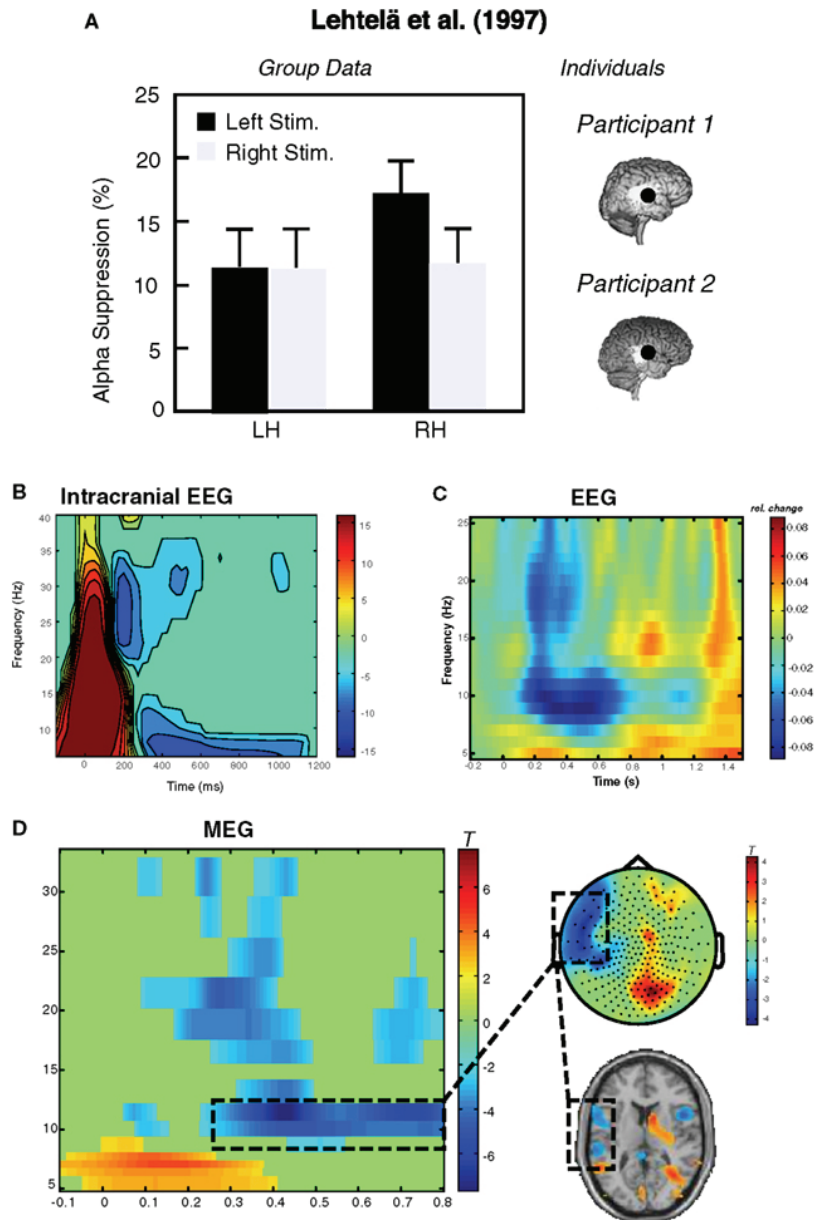


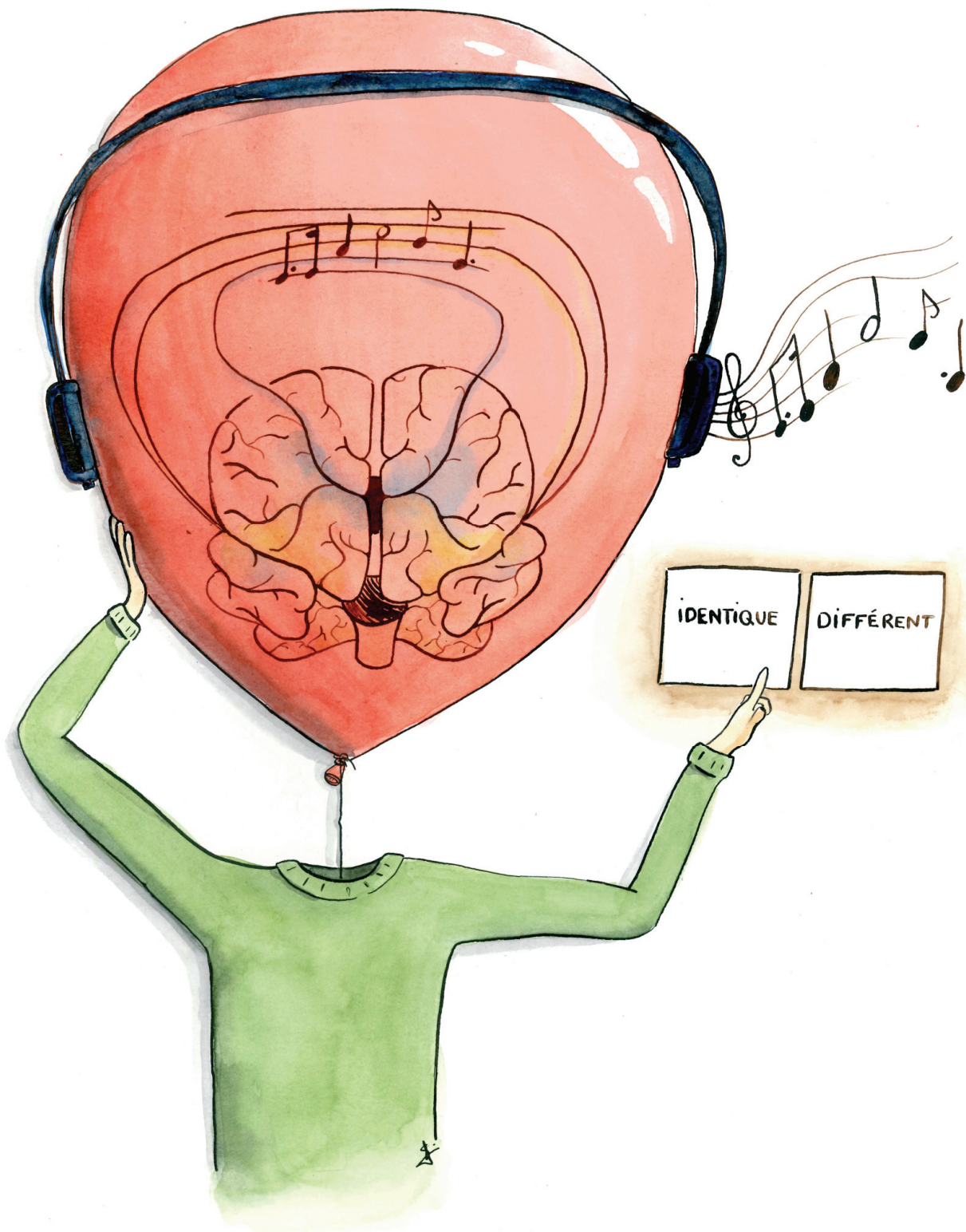
Figure 7 - Exemplary data illustrating different possibilities to record alpha dynamics from the auditory cortex. (A) Adaptation of data from the original experiment by Lehtelä et al. (1997) showing for the first time alpha suppression (6.5-9Hz) at temporal MEG planar gradient sensors during sound presentation. In two individuals (right panel), the alpha desynchronization was localized to superior temporal regions overlapping with the generators of the NI_m. (B) Single-subject data from an sEEG experiment. The depicted electrode recorded activity from primary auditory cortex, showing desynchronization between 5 and 10Hz, starting around 300ms post stimulus onset. Higher alpha desynchronizations can be observed from group data in an (C) EEG experiment and a (D) MEG experiment. In the MEG experiment, a tone was presented to the right ear, and post-stimulus decreases between 10 to 12Hz are observable over left temporal sensors, mainly in left superior temporal regions including the auditory cortex. (from Weisz et al., 2011)

3) *Specificities of pitch perception*

Several studies have focused on pitch processing in the auditory cortex using neurophysiological and neuroimaging methods in humans. As presented above, pitch information is conveyed through the tonotopic pathway which has its last relay before the auditory cortex in the thalamus (in its medial geniculate body in particular).

Several studies have shown that the tonotopic organization is preserved at a cortical level. In humans in particular, evidence was first exposed using MEG recordings (Romani et al., 1982), showing that the cortical activity in response to auditory stimuli was observed at increasing depths with increasing tone frequency. This tonotopic organization has then been confirmed thanks to various studies using different electrophysiological approaches (Howard et al., 1996; Pantev et al., 1995, 1996; Romani, 1986). Using MEG recordings, Pantev et al. (Pantev et al., 1995) showed that the amplitude of the N1 component is characterized by a reversed tonotopic organization in the *planum temporale*.

fMRI studies allowed to distinguish frequency gradients in the auditory cortex areas (Formisano et al., 2003; Langers et al., 2007; Schönwiesner et al., 2005; Talavage et al., 2000; Upadhyay et al., 2007; Woods et al., 2009). There are differences in activation between anterior and posterior Heschl's gyrus as a function of frequency (Schönwiesner et al., 2005). More precisely, there are two tonotopic gradients pointing anteromedially and posteriorly away from the long axis of Heschl's gyrus, their common low-frequency reversal extending approximately parallel to Heschl's gyrus long axis (Besle et al., 2019).



AUDITORY NON-VERBAL WORKING MEMORY

If perception is a primary step for higher cognitive treatments related to auditory information, memory can be categorized as one of these higher-level cognitive treatments. As an essential cognitive process, its impairment causes serious problems in everyday life, for construction of our self, our knowledge, and our relation to environmental information. For all these reasons, it has been extensively studied in cognitive psychology and neuroscience.

A) Memory

Memory has been defined as the capacity to acquire, retain, and use information. In the following sections, we will discuss the different models of memory.

1) *One memory or several memory systems?*

a. Historical memory models

The oldest published scientific work concerning memory seems to be from 1878. F.E. Nipher, an American physicist, published some investigations about the ability to memorize numbers better than nonsense syllables (Stigler, 1978). In this first publication, he already comments on two main memory limitations: the limited number of elements to be kept in memory as well as its decay over time. Much more details are taken into account a few years later in *Memory: A contribution to Experimental Psychology* from H. Ebbinghaus (1885), who points out that memory depends on the context, the content of the information to be memorized, and its emotional importance. He also mentions a “first fleeting grasp”, described as an immediate memory that is not sufficient for later recall. Later on, W. James (James, 1890a) formally distinguishes two types of memory; a primary memory which is capacity-limited, and a secondary memory which is an unlimited space of information that had not been compiled together in the past but are now available at any time for conscious access.

The extensive study of memory only started later, in the end of the 1950s. In 1958 emerges more refined models of an immediate memory which is called short-term memory and opposed to a long-term memory (Broadbent, 1958). However, the question of whether this distinction

should be a dichotomy or a continuum was soon brought forward (Melton, 1963). Dichotomy, as defined by Drachman and Arbit in 1966, seems to be the hypothesis of the majority (Drachman & Arbit, 1966): it is integrated in the famous model of memory established by Atkinson and Shiffrin in 1968 (Atkinson & Shiffrin, 1971), which is based on the maintenance in time of sensorial representation. According to this model, short-term memory acts as a limited buffer in which information are stored, waiting to be sent either to the long-term memory store, either to oblivion.

This dualistic model is confirmed by several brain lesions studies. It appears that patients with damages in temporal lobes and in the hippocampus have difficulties to learn and remember at long term new pieces of information (visual and verbal), even with what appears as preserved short term memory abilities (normal performances at digit span task, the task in which you have to hear and immediately repeat a series of digits) (Penfield & Milner, 1958; Pribram, 2012). In contrast, short-term memory can also be impacted due to brain lesion without any major effect on long-term memory; it was shown in the first place by Shallice and Warrington in 1970, in patients with damages in the perisylvian region of the left hemisphere (Shallice & Warrington, 1970).

Since these studies, the large majority of the community of cognitive psychology research has agreed to a multi-component model of the memory. However, an alternative homogenous theory about memory has been proposed and developed by several researchers (Crowder, 1982; MacLeod, 1979; Nairne & Dutta, 1992; Ranganath & Blumenfeld, 2005). This theory tries to take into account all types of memory with parameters explaining their length of retention among other observations. Very few studies have tried to contrast the dualistic and the monistic theories about memory (Ranganath & Blumenfeld, 2005). Henceforth, we will adopt the hypothesis for memory as a combination of multiple systems (Winkler & Cowan, 2005), in line with previous studies on auditory working memory.

b. Extensions of historical models: different memory storages

Since Atkinson and Shiffrin (1971), three main memory components have been defined: sensory memory, short-term/working memory, and long-term memory.

Sensory memory is the critical stage during which one can access perceptual information. It lasts until 10 to 20s and is directly linked to the processing of information in the perceptual system (Cowan, 1984).

Short-term and working memories correspond to a conscious access to information and corresponds to what James called “primary memory” (James, 1890a). It is capacity-limited and probably lasts for one second or two but can be maintained indefinitely through rehearsal. Short-term memory refers to the ability to maintain information for this limited amount of time, whereas the term “working memory” implies not only the maintenance but also the manipulation of the information kept in memory. Short-term and working memories are sensitive to cognitive load.

Finally, long-term memory is defined as a great capacity storage in which information can be kept for a long amount of time (from hours to a lifetime).

2) *Different stages of Memory and associated methods of investigation*

Thanks to cognitive psychology, three main stages of memory have been defined: encoding, during which accessible information is registered as memory traces; retention or storage, during which no-longer-accessible information is kept in mind over time; and retrieval, referring to the access to the information maintained so far.

During encoding, information is transcribed to a different medium which is then used by the brain cells. In neuropsychology, the usual way to study this first stage is to compare the type of information to be encoded: amount, modality, features, etc.

After encoding comes storage and maintenance of the information, for which memory traces have to be constantly updated. Poorer memory performances are observed for longer duration of retention and for larger amounts of information stored (Barrouillet & Camos, 2001; Kaernbach & Schlemmer, 2008). Therefore, this period is often reduced to no time for encoding or retrieval studies.

Finally, retrieval is the time during which there is access to previously encoded and retained information. There are two main ways to investigate retrieval: 1) recall or 2) recognition. Recall (1) means that the participant has to reproduce the stimulus presented before, either in any order they wish (free recall) or in the same order as the presentation (serial recall). Free recall appears to be harder than serial recall for long list of items, but no main difference is observed between the two options for shorter items series (Klein et al., 2005). For serial recall, accuracy is higher for first and last items, indicating an effect of primacy and underlining decay over time (which affects less the last items to be presented) (Oberauer, 2003).

During recognition (2) paradigms, participants are asked to compare a sequence of items to a reference, or to tell whether a new stimulus belongs to the reference sequence. These paradigms expect a response “identical/different” or “yes/no”. They are particularly useful for investigating items that are difficult to reproduce or describe (ideograms in the visual domain, or musical tone in the auditory modality). However, some bias emerges from these answering techniques: for example, when the difference is difficult to spot, participants will have the tendency to answer “identical” over “different”. One way to take into account such a bias is to subtract the proportion of false alarms from the proportion of hit score. Another way is to use signal detection theory (Tulving & Craik, 2005), which allows to compute two measures: the strength of the memory trace (index of sensitivity, measured by d'), and the response criterion (also called degree of caution, measured by c).

Although extensive research has been conducted on the different types of memory storage (sensory memory, long-term memory), the present chapter will focus on short-term/working memory, from their psychological concepts to their cerebral correlates, with emphasis on auditory processing. However, it should be noted that sensory, short-term/working and long-term memories are not independent. Sensory memory is essential to the encoding of information into short-term and working memory (Demany & Semal, 2008). Furthermore, long-term memory can impact working memory capacities. For example, the use of familiar items in short-term or working memory tasks improves performance in comparison with unfamiliar items (Hulme et al., 1991), underlining that previously acquired knowledge can impact perception, encoding, and retention of information. Furthermore, as mentioned above, numerous memory theories have linked short-term and long-term memories, stipulating that information stored in short-term memory is either transferred to long-term memory, either forgotten. According to Atkinson and Shiffrin, information maintenance in short-term memory should automatically generate transfer to long-term memory, but in 1972, Craik and Lockhart show that the nature and depth of the processing involved is crucial (Lockhart & Craik, 1978). Their model also implies that short-term memory is necessary for later long-term memory, which is not coherent with several neuropsychological data, in particular with patient showing deficits for short-term memory but not for long-term memory (Shallice & Warrington, 1970).

B) Working Memory

Working Memory has been defined as the cognitive ability to store and manipulate information during a limited period of time. If working memory was not distinguished from short-term memory at first, it became highly important in cognitive psychology models since the discussion of Baddeley and Hitch (1974) about some issues concerning the model of memory proposed by Atkinson and Shiffrin (1971). Baddeley and Hitch developed a new model in order to take into account these challenges. This model, refined over the years, is one of the current main models for working memory. In the following sections, we will present this model, along with other current main models of working memory from the point of view of cognitive psychology.

1) *Models of general Working Memory – Baddeley and Hitch*

Baddeley and Hitch first described a two-components system, composed of a phonological loop and a visuospatial sketchpad. This proposal was based on results showing differences between the processing of verbal and visuospatial material (Baddeley, 1966). Further investigations revealed a great impact of interference by visuospatial or verbal activities on the performance of same-modality tasks (Baddeley & Hitch, 1974; Brandimonte et al., 1992). This result led to the implementation of a third component in their model: the central executive.

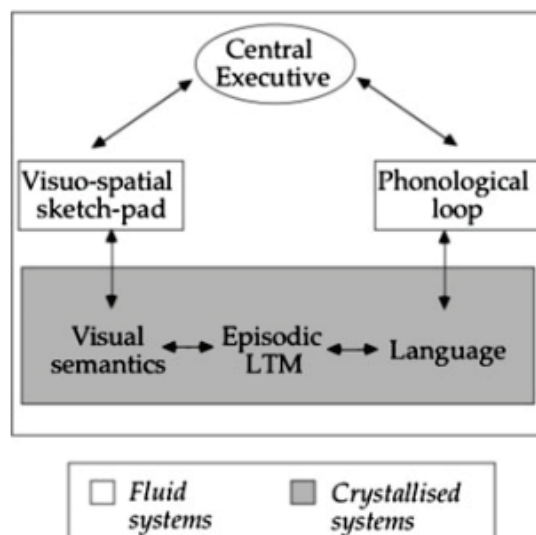


Figure 8 - Baddeley's model of working memory. LTM: Long-Term Memory. (Baddeley, 2012)

a. The phonological Loop

The phonological loop is a working-memory storage dedicated to verbal items. It is supposed to be associated with vocal or subvocal rehearsal, *i.e.* repetition of the words encoded, out loud or mentally. Removal of an item from this storage is due to a combination of trace decay and interference (as it is capacity limited, overwriting or displacement is necessary for new items to be stored). The phonological loop is affected by phonological similarity and word length: resembling words are easier to remember together, and long words are harder to retain and manipulate. This second characteristics is associated with rehearsal functioning; as rehearsal is supposed to take as long as a proper vocal repetition of a word, longer words take more time to be repeated, allowing a greater trace decay. Further studies show that the phonological loop can contain as many words as one can repeat within 2 seconds (Baddeley et al., 1975). The phonological loop is a fast and minimal-attention-needed storage for verbal items. Further studies show that it also integrates information from lip reading and signed language (Burnham et al., 2013).

b. The visuo-spatial Sketchpad

The visuo-spatial sketchpad is the working memory storage for visual and spatial information. It is not clear yet how memory traces are refreshed over time in this component. Indeed, memory of the position of a point on a line is interrupted by an information processing task, which suggest a form of active repetition (Dale, 1973). There is evidence for a partial dissociation between visual and spatial working memory within the visuo-spatial sketchpad. Furthermore, it appears that this sketchpad can also include kinesthetic memory and haptic coding (grasping, holding).

c. The central executive

The central executive component of working memory is a central component taking into account several higher cognitive processes such as attentional focus (activation of relevant items and inhibition of irrelevant information), decision making, and task switching.

d. The episodic buffer

More recently appeared a fourth component of the working memory model of Baddeley and Hitch (1974): the episodic buffer. This component is assumed to be capable of storing information in a multi-dimensional code. It has a limited capacity of 4 chunks (Cowan et al., 2005), and allows to bind elements, improving memorization. If it was first a third component controlled by the central executive, recent experiments tend to place it at the center of the model, interacting with the phonological loop and visuospatial sketchpad (Baddeley, 2000).

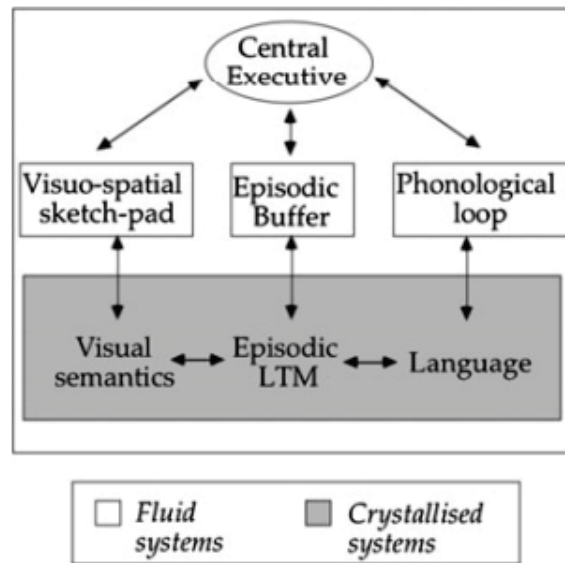


Figure 9 - Baddeley's model of working memory, recent improvements. LTM: Long-Term Memory. (from Baddeley, 2012)

2) *Models of Working Memory – Cowan*

According to Cowan (2004), working memory is composed of different cognitive processes that are maintained in an unusually accessible state. Therefore, its model is composed of a limited capacity attentional focus allowing to select areas of activated long-term memory. To Cowan, working memory is more of a use of attention to manage short-term memory.

If in theory, this model seems far removed from Baddeley's, the "limited capacity attentional focus" is very similar to the central executive component. Furthermore, some of the evidence upon which the two models are built are the same but led to different taxonomies.

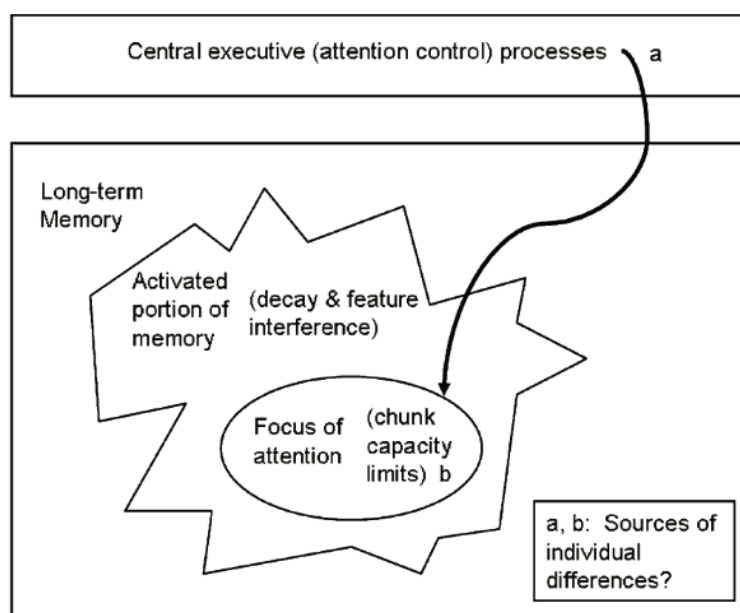


Figure 10 - Cowan's model for working memory (Cowan, 2008). Cowan depicts working memory as a portion of long-term memory activated thanks to attentional focus.

3) *Individual Difference-Based Working Memory Theories*

Another approach to working memory functioning has been to compare participants with different working memory capacities. It has been shown for example that working memory span measure can predict speech comprehension (Daneman & Merikle, 1996, 1996), going in favor of an interaction or overlap between working memory processes and general comprehension. Most of the studies involved in this prospect tend to show the importance of inhibitory processes in order to prevent memory disruptions (Barrouillet et al., 2004; Engle et al., 1999; Engle & Kane, 2004; Towse et al., 2000).

C) Working Memory for auditory non-verbal stimuli

Working Memory has long been studied using visual material, verbal or non-verbal. Later, auditory or other modality materials have been used as well, but they were mainly verbal stimuli in auditory studies. In the following sections, we will describe in more details specificities of auditory non-verbal working memory, in particular for musical stimuli (studies with other types of auditory stimuli are very scarce). Musical stimuli can vary on many levels: pitch, intensity, timbre, localization, and rhythmic components are meaningful features. We will here focus on working memory for pitch.

1) *Comparison of Working memory for tones and for words*

Several studies have focused on the comparison between working memory for tones and for words, as the first assumption of Baddeley was that music memory was processed through the phonological loop (Salamé & Baddeley, 1989). The characteristics of the phonological loop were acoustic similarity, word-length effect (capacity), and active rehearsal during retention. In the case of music, there is also an effect of acoustic similarity in non-musicians (Williamson et al., 2010). The system processing music also suffers from a limited capacity of approximately 7 to 11 notes, depending on various factors, as shown by Pembroke in 1987 (Pembroke, 1987). If several studies show no beneficial impact of rehearsal on working memory for tones (Demany et al., 2004; Kaernbach & Schlemmer, 2008; Schulze et al., 2012), these studies were using a scale of frequencies different from the western chromatic scale, which might prevent efficient rehearsal. Studies using conventional western frequencies show better working memory when participants actively practice rehearsal during retention (Koelsch, 2009; Pechmann & Mohr, 1992).

While these elements are in favor of a system similar to the phonological loop for processing musical stimuli, they do not prove them to be coincidental. In order to do so, several studies have tried to mix verbal and musical stimuli, comparing effects of heterogeneous modalities to the effects of homogeneous modalities. Concurrent speech, *i.e.* passive interference, does not affect tonal memory (Deutsch, 1970). One study compared in a systematic way short-term memory and working memory for musical sequences (pitch or timbre sequences) and verbal sequences (words); thanks to forward or backward recognition tasks (Schulze & Tillmann,

2013). Their findings suggest that the mechanisms are different for the three types of sequences: only working memory for words was sensitive to verbal active interference tasks (articulatory suppression) during the retention delay, and length effects are greater for word and pitch sequences than for timbre sequences (for a review, see Caclin & Tillmann, 2018; Schulze & Tillmann, 2013). Furthermore, in congenital amusia, working memory for musical sequences is impaired while there is no difference with control groups in terms of working memory for words (Tillmann et al., 2009).

Therefore, it seems that the hypothesis of a tonal or musical loop, as suggested by Pechmann and Mohr (1992) and Berz (1995) respectively, is the best way to model and integrate the music storage system.

2) *The musical loop*

The musical loop in its initial definition acts similarly to the phonological loop but remain a distinct system. This model has been challenged by several results which will be described and discussed in the following paragraphs.

In 1996, Semal et al. (Semal et al., 1996) showed that pitch similarity between the two materials used for memory/interference has a more important effect on memory performance than the material itself (pitch was controlled for both words and tones), suggesting either an overlap between the musical and the phonological loops, either a process of pitch memory for words outside of the phonological loop.

Several studies (Chan et al., 1998; Pechmann & Mohr, 1992) reported that musical training increases verbal memory performance, also suggesting an overlap of the loops. However, Pechmann and Mohr suggest that the overlap of the loops is function of the musical expertise: the absence of extensive training in non-musicians for music stimuli processing would be associated with more distinct mechanism of treatment for words and music, whereas the automatization of pitch processing in musicians would allow a greater overlap between the systems. Musicians have also better performance than non-musicians in working memory tasks using non-verbal auditory stimuli. They do not seem to be advantaged for most visual working memory tasks (Talamini et al., 2016), except for tasks using stimuli which are characterized by a contour (Talamini et al., 2020).

Furthermore, rehearsal of tones has been associated with activation of motor-related cortical areas, similar to the ones activated during internal rehearsal of words, confirming sensorimotor representations that can be rehearsed during memory retention (Hickok et al., 2003; Koelsch et al., 2009; Schulze, Zysset, et al., 2011). However, there is no effect of word articulatory suppression for tones (Schulze et al., 2012; Schulze & Tillmann, 2013), leading to the assumption that word and tones memory rely on different internal sensory-motor representations.

Overall, it appears that the phonological loop and the musical loop are distinct but partially overlap, as twin components of the working memory model of Baddeley.

D) Neural Correlates for auditory non-verbal Working Memory

Several studies have investigated encoding, retention and retrieval in auditory non-verbal working memory thanks to electrophysiological, MRI and TEP recordings along various tasks. These studies try to disentangle perception and working memory processes, and to underpin the specificities of non-verbal material working memory. The main questions are: is there a central brain area for tones working memory? Are there some brain markers of an efficient working memory process? In the following sections, we will present the different neuro-anatomical and functional brain responses associated with auditory working memory.

1) *A distributed Network for Working Memory*

a. Two Prefrontal Cortical Streams

It was first in 1937 that Jacobsen (Jacobsen & Nissen, 1937) tested monkeys with delayed alternation of visual stimuli, before and after removal of their entire frontal association areas. Observing greater response delays when the removal was unilateral, and a loss of the ability to answer when removing the area in both lobes, the authors deduced that the frontal region is somehow involved in memory processes. Obviously, further research projects have challenged this hypothesis, as these impaired visual memory performances might just result from deficits in multiple other processing steps such as stimulus discrimination, or even connection from reasoning to motor involvement and action (D'Esposito et al., 1999).

The study of smaller lesions of the cerebral cortex enabled to assess that there are two main streams involved in the different steps of working memory processing: the dorso-lateral and the ventro-lateral regions of the prefrontal cortex (Fuster, 1991) (see Figure 11). Lesions restricted to the dorso-lateral prefrontal cortex (DLPFC) were shown to be sufficient to produce working memory deficits in monkeys (Blum, 1952). Neuro-imaging studies comparing memory and non-memory tasks have extensively shown that the DLPFC and the ventro-lateral prefrontal cortex (VLPFC) are involved during encoding and maintenance steps of working memory (Arnott et al., 2005; Curtis & D'Esposito, 2003; D'Esposito et al., 1995; Nystrom et al., 2000; Owen, Morris, et al., 1996; Postle & D'esposito, 2000; Sala & Courtney, 2007; Wager & Smith, 2003).

The activated DLPFC area has even been restricted to the anterior DLPFC (Huang et al., 2013), a region that has been shown to be extensively connected to the antero-lateral belt of the auditory cortex (Kaas & Hackett, 1999; Romanski et al., 1999). The main question was then to specify the role of these two sub-regions (DLPFC and VLPFC).

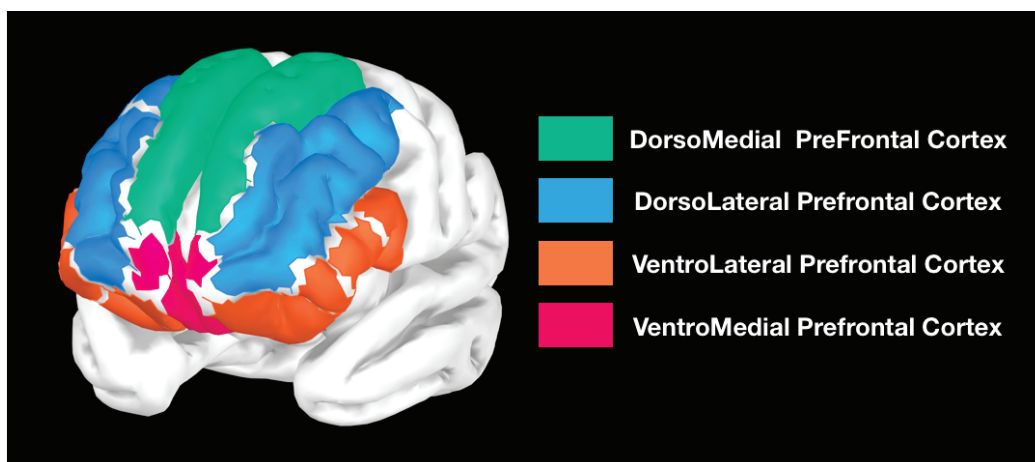


Figure 11 - The Prefrontal Cortex and its subdivisions. (original figure computed with brainstorm (Tadel et al., 2011), thanks to the Desikan-Killiany atlas (Desikan et al., 2006))

Initial results showed that the DLPFC is related to spatial information, whereas the VLPFC is mainly recruited during maintenance of non-spatial information (D'Esposito et al., 1995; Levy & Goldman-Rakic, 2000; Sala et al., 2003). These results support the view according to which elements to be encoded are treated in different brain streams according to the type of information they contain, which fits nicely with the phonological loop and visuo-spatial sketchpad proposed in Baddeley's model (Baddeley, 2000). However, these initial results have been challenged by numerous studies which failed to observe a contrast between object versus

spatial information (Deouell et al., 2007; Owen, Evans, et al., 1996). Studies implying active rehearsal during the maintenance period, in contrast with passive or absence of rehearsal have revealed an increasing activation of the VLPFC during active rehearsal (Khan & Muly, 2011; Owen, Evans, et al., 1996), implying that VLPFC's role would be limited to simple, executive maintenance in memory. In 2003, Wager and Smith (Wager & Smith, 2003) published a meta-analysis reporting evidence for a dedicated role of the DLPFC as an executive center in charge of highly demanding processes involved in working memory such as the monitoring of the different areas involved (depending of the modality solicited) or the manipulation of the information. This second proposal fits easily the model of Baddeley, with the DLPFC as the central executive, and the VLPFC as a stream recruited by the different buffers during memory maintenance.

b. Other brain regions involved in auditory working memory

(i) Posterior Parietal Cortex

If the DLPFC and the VLPFC are prominent regions activated during working memory, they are not the only ones. Initially, the posterior parietal cortex (PPC) was identified as the working memory store supporting maintenance (D'Esposito, 2007; D'Esposito et al., 1999; Smith & Jonides, 1998; Wendelken et al., 2008) and retrieval (Berryhill et al., 2011) of the information. By comparing difficulties in working memory encoding in schizophrenic patients to normotypical participants, Manoach and collaborators showed that encoding is also based on the activity of posterior parietal regions, as well as the cingulate and basal ganglia and the hippocampus (Manoach et al., 2000). Champod and Petrides (2010) showed that the PPC, and in particular the Intra-Parietal Sulcus (IPS) is involved in manipulation of the information, while the DLPFC has a role in monitoring the information being manipulated (see also Warrier & Zatorre, 2002).

(ii) Auditory cortex

The involvement of the visual cortex in visual working memory has been clearly established thanks to several human neuroimaging studies (for a review, see D'Esposito & Postle, 2015; Pasternak & Greenlee, 2005; Postle et al., 2004). In the auditory domain, the involvement of primary auditory cortex in auditory working memory is not consensual. In a two-tones maintenance task, Linke and colleagues pointed out a suppression of fMRI activity in the auditory cortex (Linke et al., 2011) whereas Leiberg and collaborators showed increased activity in the right middle prefrontal cortex and in the right temporal cortex during working

memory maintenance (Leiberg et al., 2006). The maintenance of a complex sound in memory has been associated with an increased fMRI activity in the auditory cortex (Linke & Cusak, 2015). The maintenance of pitch by participants with pitch memory impairments revealed a decreased activity in the right auditory cortex, inferior frontal gyrus (IFG) and dorso-lateral prefrontal cortex; and of the right-lateralized functional connectivity between the auditory cortex and the IFG during tonal encoding (Albouy et al., 2019). Two other studies focused on a delayed match to sample task for sequences with interfering songs; one, with fMRI, showed increased activity in the auditory cortex (Gaab et al., 2003), while the other using PET showed decreased cerebral blood flow in the region of the auditory cortex (Zatorre et al., 1999).

In order to resolve this challenging debate, several studies have tested different paradigms using different neuroimaging techniques (EEG, fMRI, PET, MEG) and have finally shown a clear interaction between the auditory and motor cortices, revealing that musical tones are internally translated into sensorimotor representations that can be rehearsed (Hickok et al., 2003; Koelsch et al., 2009; Schulze, Zysset, et al., 2011; Tsai et al., 2018).

An increase of connectivity between the auditory cortex and the inferior frontal cortex and hippocampus have been interpreted by Kumar and colleagues as a projection of the information on higher order processes (Kumar et al., 2016). Furthermore, multivoxel pattern analysis showed that patterns of activation in the auditory cortex and the inferior frontal gyrus can differentiate different encoded tones (Kumar et al., 2016).

(iii) Medial Temporal Lobe

Encoding is partially based on the activity of the hippocampus, in direct link with the analysis of auditory stimuli in real time, via auditory-hippocampal connections (Albouy et al., 2019; Kumar et al., 2016; Manoach et al., 2000). Moreover, parahippocampal lesions in monkeys leads to poorer performances of working memory (Eacott et al., 1994; Eichenbaum et al., 1992). However, this effect is specifically linked to the treatment of novel stimuli.

(iv) Striatum

Striatum has been shown to be involved in working memory for verbal auditory items (Lewis et al., 2004), but not for tonal items. It is more linked to reward expectations and thus to attentional focus rather than to information maintenance (Kawagoe et al., 1998).

Taken together, all these studies revealed a distributed network involved in encoding, maintenance and retrieval steps of auditory non-verbal working memory, for diverse sub-

processing of the information (monitoring, storage, update, focus of attention). Observations converge towards the idea of a recruitment of frontal cortical and posterior temporal areas, and their interaction, which is quite similar to the visual working memory network. The cortical regions recruited by working memory for pitch could be seen as a specialized subsystem within the framework of general working memory (Janata et al., 2002; Peretz & Zatorre, 2005).

The dynamics of this network has been investigated in many ways in order to better understand its functioning, which will be described in the following section.

2) *Electrophysiological markers of Working Memory*

a. Event-Related Potentials/Fields related to Working Memory for pitch

Several modulations of the classical ERs elicited during sound perception are observed during working memory.

Comparing ERs before and after training of working memory on pitch reveals an increase of the evoked potential N1 (Li et al., 2015). Study of impaired short-term memory for pitch in congenital amusia revealed that encoding inability includes N_{100m} (magnetic equivalent of N₁₀₀) modulation: the amplitude of the N_{100m} is decreased in congenital amusics (Albouy et al., 2013). Its generators lay in the bilateral fronto-temporal network.

When comparing the encoding of sounds during Hit and Miss trials, Fernandez-Duque showed that there is a late positive drift (Fernandez-Duque et al., 2000) starting from 500 to 600 milliseconds after the onset of the presented sound, which they called “Dm” effect. The Dm effect is supposed to be generated by para-hippocampal and hippocampal generators and has been shown later on by Friedman and colleagues (Friedman & Johnson, 2000; Friedman & Trott, 2000) to be linked with left inferior prefrontal activation.

Another slow ER has been revealed when comparing different working memory loads, called the Sustained Anterior Negativity (SAN): the SAN appears during working memory maintenance and increases for increasing loads (Alunni-Menichini et al., 2014). The SAN can be elicited for both pitch and timbre features (Nolden et al., 2013). Its generators are distributed in the bilateral superior temporal, the superior parietal, and the frontal cortices (Bella et al., 2009). The frontal component of the SAN can be elicited with visual and verbal stimuli but is significantly less important than for musical tones (Asenbaum et al., 1992; Nolden et al., 2013).

Finally, the prolonged activation or reactivation of brain regions underlying perceptual processing of pitch (see section Memory) during the retention period is interpreted as a way to refresh neural traces of the encoded stimuli (Grimault et al., 2014).

b. Oscillations and Working Memory

The main oscillatory band associated with auditory working memory is the gamma band (>30Hz). It has first been associated with general objects representation, attention, and memory (Jensen et al., 2007; Kaiser et al., 2003), but in particular with visual working memory (Jensen et al., 2007; Kaiser et al., 2003; Tallon-Baudry et al., 1999). Its power increases significantly in the prefrontal cortex during the working memory retention phase for tones length information (Jensen et al., 2007). Encoding deficits in congenital amusia are associated with a lower gamma-band power in the right dorsolateral prefrontal cortex during pitch sequence retention (Albouy et al., 2013).

The power of right-sided temporal beta oscillations (15-30Hz) correlate positively with memory load during working memory maintenance, which can lead to the hypothesis that it helps dealing with larger amount of information (Leiberg et al., 2006). However, a recent study using intracranial EEG in monkeys revealed that beta bursting might reflect a default network state interrupted by gamma during encoding and re-encoding (Lundqvist et al., 2016). The analysis of beta modulations after pauses in a cognitive task show that there is a reset, thus suggesting that beta oscillations might reflect multiple factors contributing to the regulation of cognitive control (Stoll et al., 2016).

Another frequency band that has been associated with demanding cognitive task is the alpha band (7-15Hz) (Buzsáki, 2005). The power of right frontal alpha oscillations increases during maintenance of auditory verbal or non-verbal stimuli (Jensen et al., 2007; Leiberg et al., 2006; Luo et al., 2017; Van Dijk et al., 2010). This increase is correlated negatively with memory load (Leiberg et al., 2006; Sauseng et al., 2005, 2009): once again, frontal activity is linked to the ability of monitoring the amount of information stored in memory, and to the reactivation of memory traces (Bonfond & Jensen, 2012; Palva et al., 2010; Palva & Palva, 2011).

Finally, power and phase of theta oscillations (4-8Hz), associated with coherent long-range communication and synchronicity along fronto-parietal regions, are very sensitive to working memory manipulations in all steps of working memory (Albouy et al., 2017; Fell & Axmacher, 2011; Polanía et al., 2012; Sauseng et al., 2010).

As presented in the previous section, musical expertise has been shown to be associated with highly better short-term and working memory performances for non-verbal auditory stimuli (Talamini et al., 2017, 2020). Therefore, several studies have focused on the differences of brain activity between professional musicians and non-musicians.

3) *Influence of musical expertise*

If everybody engages in some musical activities in everyday life, it is mainly limited in time and effort. In contrast, few individuals playing music regularly and with explicit tutoring in different educational systems creates a diversity of musical expertise which is a unique model to study plastic changes in the brain (Münte et al., 2002).

It has been proved through animal research that experience can shape the size of a cortical network, either positively (expansion) or negatively (reduction) (Münte et al., 2002). Hence, we could expect that musician's brain exhibit an enlargement of the motor and auditory areas, but maybe also of some components of the working memory network. Indeed, studies show that there is clear evidence for the grey matter volume of the motor cortex of musicians to be enhanced (Gaser & Schlaug, 2003; Krings et al., 2000), just as long as motor-related structures like the cerebellum and the corpus callosum (Hutchinson et al., 2003).

The structure of the auditory cortex is also modified by musical practice: both the early activity evoked by pure tones and the volume of the grey matter of the anteromedial portion of Heschl's gyrus were more than doubled in professional musicians than in non-musicians (Schneider et al., 2002). The VLPFC, the left insular cortex, the cingulate gyrus, and the left intra-parietal lobule are activated more strongly in musicians compared to non-musicians in pitch working memory tasks, and musicians activate specific subcomponents only during verbal (right insular cortex) or only during tonal working memory (right globus pallidus, right caudate nucleus, and left cerebellum) (Schulze, Zysset, et al., 2011). One commonly accepted hypothesis is that musicians use the non-musicians' verbal network for tonal information. Musicians also seem to have elaborated sensory-motor codes allowing them to have better inner representations of tones and to rehearse them better in memory (Schulze et al., 2011; Schulze et al., 2012).

Conclusion

In this chapter, we presented a brief overview of the behavioral and cerebral correlates of auditory non-verbal working memory. We have presented the historical line leading to the accepted mosaic of memories and explored the different behavioral studies characterizing working memory as a concept and as a process. We have underlined that working memory is a capacity-limited process requiring brain resources in a widespread fronto-parieto-temporal network. This capacity limitation implies a choice in the information to be memorized. In order to be efficient in a task, one must distinguish relevant and irrelevant information, and filter what needs to be ignored. This ability to ignore what is not important is part of a main cognitive function that is called attention.



AUDITORY SELECTIVE ATTENTION

In 1980, William James was convinced that “everyone knows what attention is” (James, 1890b). We might all have a more or less blurry idea of what is attention, but words to define it can help: attention is commonly defined as a cognitive process allowing us to focus on one part of the available information while ignoring other elements in our direct surroundings. During every moment of our life, numerous external and internal events are competing for neural representation (Gaspelin et al., 2013). Our brain has to face these events with its limited processing capacity: it relies on attentional processes to prioritize the processing of only a part of the surrounding information (Desimone & Duncan, 1995; Reynolds & Heeger, 2009).

There are different ways to study attention, and different frameworks have emerged along time. In some situations, attention can be an involuntary process, triggered by external salient stimuli. Involuntary processes can be helpful, for example in detecting danger even when we are not on the lookout. In contrast, there are other situations in which attention can be a voluntary process. During the COVID-19 quarantine, everyone was waiting for precise information on the lockout, on the opening of public structures, on the return to work, and so on. Therefore, during official governmental speeches, we were focused in a sustained manner, until we could detect the first word, "restaurant", for example, which would tell us the information we were waiting for. This is an example of sustained attention, which is evaluated in laboratories thanks to go/no-go experiments, in which participants are required to pay attention until the information for motor response (or not) appears.

During the speeches of officials, there may be noise around us, distracting elements, or a person asking us a question. Divided attention is the process allowing us to focus on several streams of information, therefore paying attention to both speech streams, while selective attention is the process allowing to inhibit irrelevant distracting elements in favor of relevant streams of information.

In our experimental set-up, we focused on selective attention. Selective attention refers to the capacity to pay attention to one source of information while inhibiting other sources that are judged as irrelevant (Hillyard et al., 1973).

A) Psychological models of selective attention

Selective attention is crucial for selecting relevant information and filtering out distracting elements. Thanks to this process, you can deliberately focus on reading this manuscript and not on the noise that surrounds you, or should I hope so: you are selecting, between two sources of information, one to ignore and one to focus on.

Selective attention has been formalized thanks to structural models, based on the assumption that attention has a limited capacity, and that the selection of the information is made at a specific moment of the analysis, the question being “when exactly does this selection happen?”

1) *Early-selection theory of selective attention*

The main paradigm to study selective attention is dichotic listening. In dichotic listening experiments (see Figure 12), participants are exposed to two auditory streams, each presented in one ear. Participants have to focus their attention on one ear while ignoring the other (Broadbent, 1958; Cherry, 1953; Hillyard et al., 1973). The indication to the target ear can be given at the beginning of each trial, of each block, or implied by contrast between the characteristics of the two streams. Selective attention has been extensively studied thanks to verbal or non-verbal auditory stimuli.

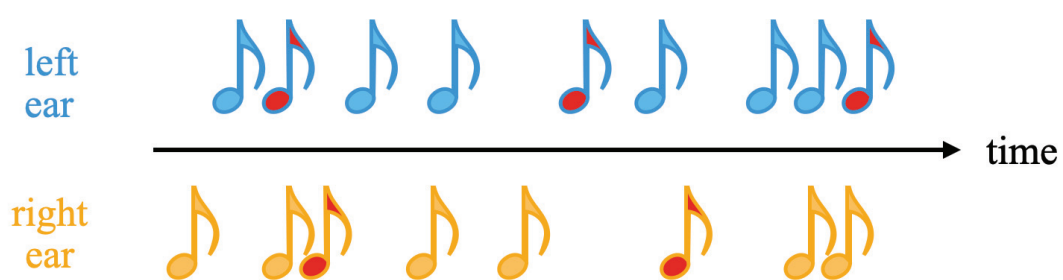


Figure 12 - The dichotic listening paradigm. Participants are told to detect deviant sounds in a sound stream played in one ear while ignoring a sound stream played in the other ear. The ear to focus on is indicated by a cue (such as a visual arrow indicating the right ear). Deviant sounds (in red) can be played in both attended and unattended ears. Only deviant sounds in the attended stream are targets to be detected.

One of the main issues relative to selective attention is to understand at which stage of processing the selection of relevant information is performed. Initial results showed that participants did not process the stimuli displayed in the ignored ear (Broadbent, 1958), thus enabling the formulation of the early selection theory. Encoding irrelevant sources of information could be blocked before its completion. Elementary physical properties of the stimuli would be encoded and analyzed in parallel, and only a selected channel of information would access higher cognitive levels (Broadbent, 1958). Later, this result have been nuanced: studies showed that a fragment of the unattended irrelevant stream of information was still processed in depth; participants could tell when their own name was presented in the ear they were ignoring (Moray, 1960). This led to (1) the modification of the early selection theory, in which the unselected channel of information was attenuated instead of entirely rejected (Treisman, 1960), and (2) the emergence of the late-selection model for selective attention.

2) *Late-selection theory of selective attention*

In the late-selection model for selective attention, it is only after the encoding of all stimuli that the selection is made to decide which information gains access to higher cognitive treatment (Deutsch & Deutsch, 1963; Norman, 1968). The role of selective attention is in this case to control access to consciousness, and memory encoding for example. Evidence for this model come from slightly different paradigms, with less difficult tasks in particular, such as dichotic listening with a slow stimulus rate, or other selective-set paradigms such as visual search (W. Schneider & Shiffrin, 1977).

This opposition of easy versus difficult tasks and their associated contributions to late or respectively early selection theories led to the emergence of another class of selective attention theories, based on the amount of resources available for attention.

3) *Load theories of selective attention*

The early/late selection debate resolution leads to a more unified vision of both early and late selection theories. Under low perceptual load, *i.e.* with a low amount of perceptual capacities devoted to relevant information processing, distractor processing seems reduced at later processing stages, whereas when processing of task-relevant stimuli involves high perceptual load, distractor processing can be reduced at early stages (Cartwright-Finch & Lavie, 2007; Forster & Lavie, 2007; Handy & Mangun, 2000; Huang-Pollock et al., 2002; Lavie, 1995; Lavie et al., 2014; Lavie & Cox, 1997; Lavie & Tsal, 1994).

One way to play on perceptual load, in the auditory modality, can be the use of different physical properties of the sounds: the closest the physical properties of the sound are, the hardest it is for participants to segregate the two streams of information at a perceptual level, the hardest it is for them to focus on only one ear and ignore the other one (Woods et al., 2001).

Interference load can be perceptual, but it also can be cognitive (Lavie et al., 2004; Lavie, 2005; Yi et al., 2004). According to the cognitive load theory, under low cognitive load (*i.e.* when a low amount of cognitive and executive resources is allocated to a cognitive task) resources are numerous enough to be involved in efficient attention filtering. Under high cognitive load, limited cognitive resources can lead to the incapacity to filter correctly distracting information.

B) Physiological models of selective attention

Another approach to study auditory selective attention was to focus on event-related potentials (ERPs). ERPs have a temporal specificity allowing to measure time events occurring before a behavioral answer, which allows to access precise information on the temporal dynamics of cognitive processes. They also have specific topographies that help to decipher which structures and neurophysiological processes are involved.

ERPs were an important tool to provide definitive electrophysiological support for the early-selection theories of attention, but the question remained of how early and by which physiological mechanisms attentional selection occurs. In order to answer these questions, dichotic paradigms have been thoroughly used. It appears that ERPs to unattended tones were reduced compared to ERPs to attended tones (see Figure 13). This observation led to two interpretations developed as two different physiological models of auditory selective attention.

1) *The gain theory of attention*

Broadbent and Treisman proposed that selective attention works as a *gain mechanism* able to inhibit or gate unattended stimuli in comparison with attended stimuli, at an early stage of sensory analysis, as revealed by an enhanced N1 for attended versus unattended stimuli. This N1 effect was interpreted in this case as an increased activity of the N1 generators, implying a modulation of activity of the neurons involved in the sensory analysis of acoustic stimuli in the auditory cortex (Broadbent, 1958; Treisman, 1960).

2) *The attentional trace model of attention*

Later, it was suggested by Näätänen that this N1 effect was caused by an endogenous processing negativity, observed when subtracting ERPs to ignored tones from ERPs to the same unattended tones (Näätänen & Michie, 1979). This processing negativity (PN) would overlap the exogenous N1, and therefore create this enhanced N1. It appeared to be composed of an early component associated with the auditory cortex, and a late component, longer and larger, associated with frontal sites. These observations led to the emergence of the attentional trace model of attention, according to which the initial selection is performed by a comparison process between a sensory input and an attentional trace in auditory cortex. This attentional trace would be a representation of the differences between targets and distractors at the level of physical features, voluntarily held thanks to a consciously controlled system. The early PN could reflect the comparison mechanism, whereas the late PN could reflect a frontal mechanism consciously controlling and maintaining the attentional trace (Naatanen, 1992; Näätänen, 1982, 1990).

C) Neural correlates of selective attention

In the previous sections, we attempted to define selective attention from a psychological and physiological point of view. Here, we discuss about the underlying brain network, and the electrophysiological modulations induced.

1) *A distributed network of selective attention*

Much of the knowledge about attention networks comes from investigations in the visual domain. Therefore, we will discuss studies from visual and auditory modalities. The control of selective attention requires the organism to target one sensory dimension for focus, while inhibiting others. This, in theory, should be associated with a cognitive system controlling the attentional shift, the engagement and disengagement operations. These operations should then produce subsequent changes in the cortical areas dedicated to relevant information processing (Posner & Dehaene, 1994). This hypothesis has been thoroughly tested thanks to the different paradigms presented above, along with brain recordings.

As the networks of visual and auditory attention are very intricate, the core networks of selective attention might be considered as supramodal (Macaluso et al., 2003, 2005; Macaluso, 2010). One main region associated with visual and auditory domains is the prefrontal cortex, represented in Figure 11 (Alho et al., 2014; Buschman & Miller, 2007; Chao & Knight, 1995; Corbetta et al., 2008; Katsuki & Constantinidis, 2004.; Miller & Cohen, 2001; Salmi et al., 2009b).

Studies in the visual modality on human and non-human primates, in fMRI and PET, revealed the existence of two main hubs for selective attention: the Intra-Parietal Sulcus (IPS) and the Frontal Eye Field (FEF) (Corbetta et al., 1993; Corbetta et al., 2000; Corbetta & Shulman, 2002; Kastner et al., 1999; Nobre et al., 1997; Shulman et al., 2010; Wardak et al., 2006; Wojciulik & Kanwisher, 1999). Trans-cranial Magnetic Stimulation (TMS) targeting these two regions succeeded in disturbing the focus of attention of the participants (Szczepanski & Kastner, 2013).

Studies in the auditory domain tend to underline that auditory and visual selection attention mechanism rely on similar core brain networks (Shomstein & Yantis, 2004; Smith et al., 2010). However, several supplementary regions seem to be involved in auditory mechanisms, such as the dorso- and the ventro-lateral prefrontal cortex (Juha Salmi et al., 2009; Voisin et al., 2006).

The lateral prefrontal cortex (laPFC, *i.e.* VLPFC and DLPFC, see Figure 11) has been shown to play a role in supporting the voluntary network by enhancing the relevant sensory modality pathway activation and inhibiting the irrelevant sensory modality pathway activation (Caclin & Fonlupt, 2006; Greenberg et al., 2010).

The laPFC has also been shown to be involved in attentional capture in both auditory and visual modalities. Its activation is correlated with distractors inhibition and its reduced activity is correlated to impaired distraction processing (Han & Marois, 2014; Möttönen et al., 2014; Suzuki & Gottlieb, 2013), which implies its importance in selective attention. It remains unclear whether the laPFC is involved in the attentional capture itself, or in attention reorientation control towards the relevant information, or in the inhibition of irrelevant information.

2) *Selective attention modulations of auditory responses*

Practically all the different late-latency ERPs associated with sound processing are impacted by attention. Initial electrophysiological investigations showed that sound processing is impacted starting from 50ms after its onset presentation (Hansen et al., 1983; Hillyard et al., 1998; Woods et al., 2009), and even from 20ms after its onset (Bidet-Caulet et al., 2007; Woldorff et al., 1993, 1997; Woldorff & Hillyard, 1991).

a. P50

Several studies report an enhancement of the early latency potential P50 amplitude to an attended in comparison to an unattended sound in dichotic listening paradigms (Hackley et al., 1990; Hillyard et al., 1973; Woldorff et al., 1993). On the contrary, several studies report an absence of effect on the P50; it is commonly accepted that the more difficult the task is, the earlier the effect is present (Giard et al., 2000).

Lesion studies showed that damage in the dorsolateral prefrontal cortex leads to an increase of the middle latency EPs (such as the P50) associated with distractors processing. This reveals the presence of an active inhibition of the irrelevant sounds generated by the frontal cortex upon the primary auditory cortex or perhaps on the thalamus (Chao & Knight, 1995; Knight et al., 1999).

P50 amplitude has been shown to be reduced for the second stimulus of a pair, a phenomenon called P50 gating; this decrease has been shown to be indifferent to selective attention variation (Guterman et al., 1992; Jerger et al., 1992; Kho et al., 2003).

b. N1

As mentioned above, and illustrated in Figure 13, the N1 is enhanced in response to attended compared to unattended stimuli (Bidet-Caulet et al., 2007; Fujiwara et al., 1998; Hansen & Hillyard, 1980; Steven A. Hillyard et al., 1973; Kho et al., 2003; Näätänen & Picton, 1987; Neelon et al., 2006; Okita, 1979; Parasuraman et al., 1989; Picton & Hillyard, 1974).

Selective attention also modulates its magnetic counterpart, the M100, which was localized to the auditory cortex on the supratemporal plane, just lateral to Heschl's Gyrus (Lee et al., 2014; Woldorff et al., 1993) (see Figure 14).

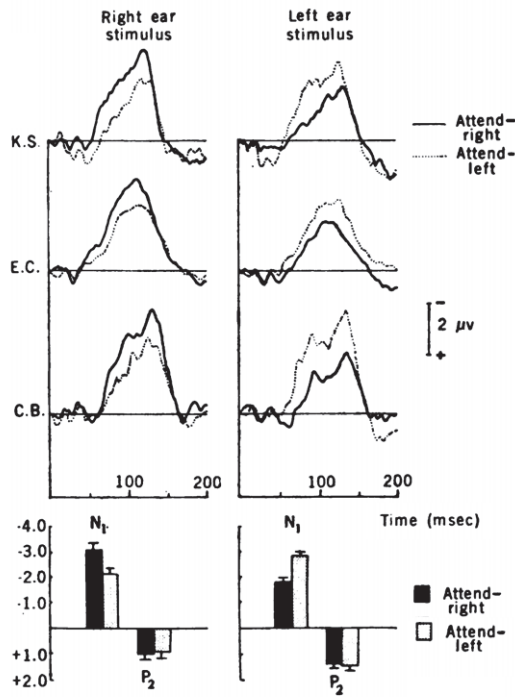


Figure 13 - Vertex evoked potentials from three subjects performing the dichotic task. Each tracing is the averaged response to all 1024 stimuli that were presented to each ear under attend-right (solid lines) and attend-left (dotted lines) conditions. Stimulus onset is at beginning of tracing, baselines were drawn through the mean voltage over 0 to 10 msec. (Adapted from Hillyard 1973)

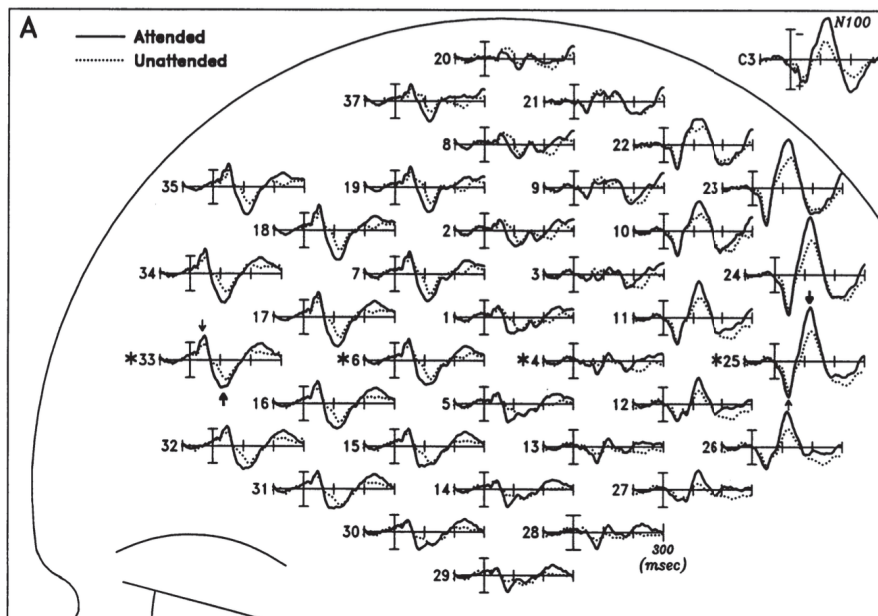


Figure 14 – Waveforms averaged across seven subjects of the event-related magnetic activity elicited by right-ear standard tones when they were attended (continuous line) in comparison with unattended (dotted line). They are displayed at approximate locations of the magnetic sensors over the left hemisphere. At the upper right are the simultaneously recorded ERPs from the C3 site. MEG: positive (upward) values indicate that the fields are directed out of the head (calibration bar: +20 fT). EEG: negativity is plotted upward (calibration bar: 1μV). Large arrows mark the polarity inverting M100 at sites 25 and 33, small arrows denote the polarity-inverting MS0 (from Woldorff et al., 1993).

c. Sustained Evoked Responses

Sustained auditory evoked responses are enhanced for attended compared to unattended stimuli (Bidet-Caulet et al., 2007; Ross et al., 2004). However, this is not observed when the attentional selection is easy (Dean Linden et al., 1987).

3) *Oscillations and selective attention*

Two main oscillatory rhythms have been shown to be impacted by attention variations: alpha (5-15Hz) and gamma (>30 Hz) oscillations.

a. Alpha oscillations

The correlation between visual alpha power and attentional task performances has been shown in some studies. Pre-target alpha power decrease correlates with a decrease of reaction time to target, *i.e.* when the attention is oriented toward a visual target, the inhibition of the visual cortex is reduced, allowing to be more efficient and detect the target in a faster way (Bonfond & Jensen, 2015; Thut et al., 2006). A coordinated alpha desynchronization in the occipital area contralateral to the irrelevant item (Doesburg et al., 2016; Kelly et al., 2006; Marshall et al., 2015; Rihs et al., 2007, 2009; Thut et al., 2006; Worden et al., 2000) suggests that in the same time, the brain areas that are not relevant for the task see their level of inhibition increase, leaving more resources to the needed areas. This means that alpha plays a very important role in selective attention, helping to inhibit or facilitate different parts of available information. Furthermore, several experiments report enhanced auditory alpha desynchronization with auditory selection (ElShafei et al., 2018; Frey et al., 2014; Tervaniemi & Hugdahl, 2003; Weisz et al., 2011, 2014), see an example in Figure 15.

To identify the higher order command on alpha, several connectivity analyses were led. Thanks to a brief interference created by repetitive transcranial magnetic stimulation (rTMS), with preparatory activity in right intraparietal sulcus (IPS) or right frontal eye field (FEF) while subjects attend to a spatial location, Capotosto and colleagues showed a behavioral effect (impaired identification of target visual stimuli around 2s later) supported by a disruption of prestimulus alpha desynchronization. This results supports the interpretation according to which fronto-parietal regions, in particular the IPS and the FEF would control alpha oscillations in visual regions (Capotosto et al., 2009), and therefore would control at least partly selective attention.

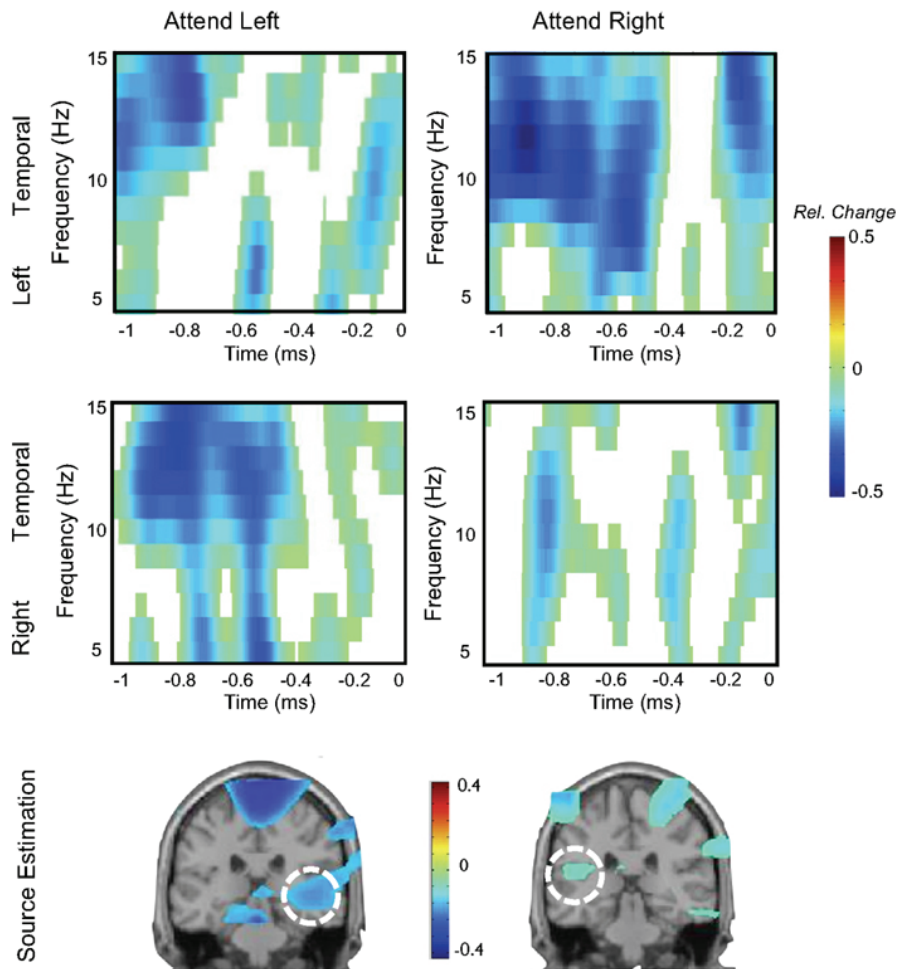


Figure 15 – Single-subject data revealing modulations of auditory alpha by spatial attention. Upper two panels: time-frequency representations of left and right temporal sensors respectively, while anticipating an upcoming auditory target on the left or right ear (at time-point 0). Modulations are asymmetric, with stronger desynchronization at left sensors when attending to the right ear, and vice versa for right sensors. Source analysis implies the involvement of auditory cortex in this effect. Please note that the cue was visually presented. (from Weisz et al., 2011)

A recent emerging question about alpha is its sub-division in different frequency bands. Indeed, the alpha band was first divided into three sub-bands, associated with different attentional processes: phasic alertness from 5 to 8 Hz, expectancy from 8 to 12Hz, and task performance from 12 to 15Hz (Klimesch et al., 1993; Klimesch et al., 1998; Klimesch, 1999). However, the current studies on alpha mainly describe alpha as a united indivisible band. Recent results show that alpha peak frequency could be considered as a variable feature across individuals and their characteristics such as age, neurobiological particularities or behavioral performances (Başar, 2012; Klimesch, 1999), but also variable across cortical regions (alpha desynchronization in the auditory cortex peaks around 8-9Hz, while synchronization in the visual cortex during an auditory task peaks around 11-12Hz) (ElShafei et al., 2020; ElShafei, Bouet, et al., 2018; Haegens et al., 2014).

The combination of results from EEG, MEG, MRI, connectivity measures (coherence, phase locking, granger causality) in the auditory domain (Weisz et al., 2011, 2014) showed that alpha synchronization could play a role in the coordination and regulation of neural processing across fronto-parietal and auditory system. For example, a stronger phase synchrony has been observed between the contralateral auditory cortex and the IPS and IPL during auditory spatial attention tasks (Huang et al., 2014; Weisz et al., 2014).

Auditory selective attention impact on the activation of brain regions dedicated to other modalities such as vision: there is an increase of occipitoparietal alpha power during auditory attention, which has been interpreted as an inhibition of irrelevant visual processing (ElShafei et al., 2018; Foxe & Snyder, 2011; Frey et al., 2014; Fu et al., 2001). This result suggests a potential supramodal attention control system (Barnerjee et al., 2011; Frey et al., 2014).

b. Gamma oscillations

The association between gamma-band activities and attentional processes follow almost the opposite of alpha oscillations: gamma power in the auditory cortex is enhanced for voluntarily attended auditory stimuli (Debener et al., 2003; Zaehle et al., 2009).

In the visual domain, gamma power correlates with behavioral performances to target detection tasks: increase of gamma amplitude is associated with faster responses (Fründ et al., 2007; Gonzalez Andino et al., 2005; Martinovic et al., 2007; Schadow et al., 2009). Increase of gamma amplitude has also been associated with faster (Ahveninen et al., 2013) and better (Ahveninen et al., 2013; Kaiser et al., 2003) performance in the auditory domain. Gamma power in the lateral prefrontal cortex has been shown to be a reliable index of attentional performance (Rouhinen et al., 2013). Top-down attention has been shown to increase gamma synchrony between frontal regions and task-relevant regions (Baldauf & Desimone, 2014; Gregoriou et al., 2009).

Gamma phase synchronization and induced response gamma power both increase under selective somatosensory attention in the prefrontal and parietal cortices (Desmedt & Tomberg, 1994; Gobbelé et al., 2002). Induced gamma activity increases in occipital electrodes for attended visual stimuli compared to unattended ones (Keil et al., 1999; Müller et al., 2000).

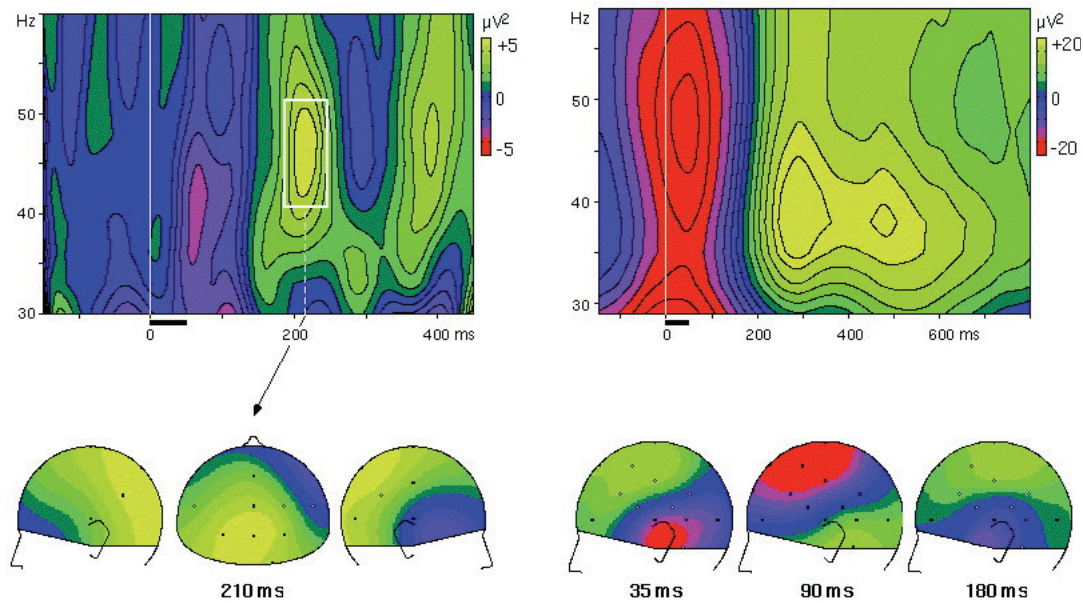


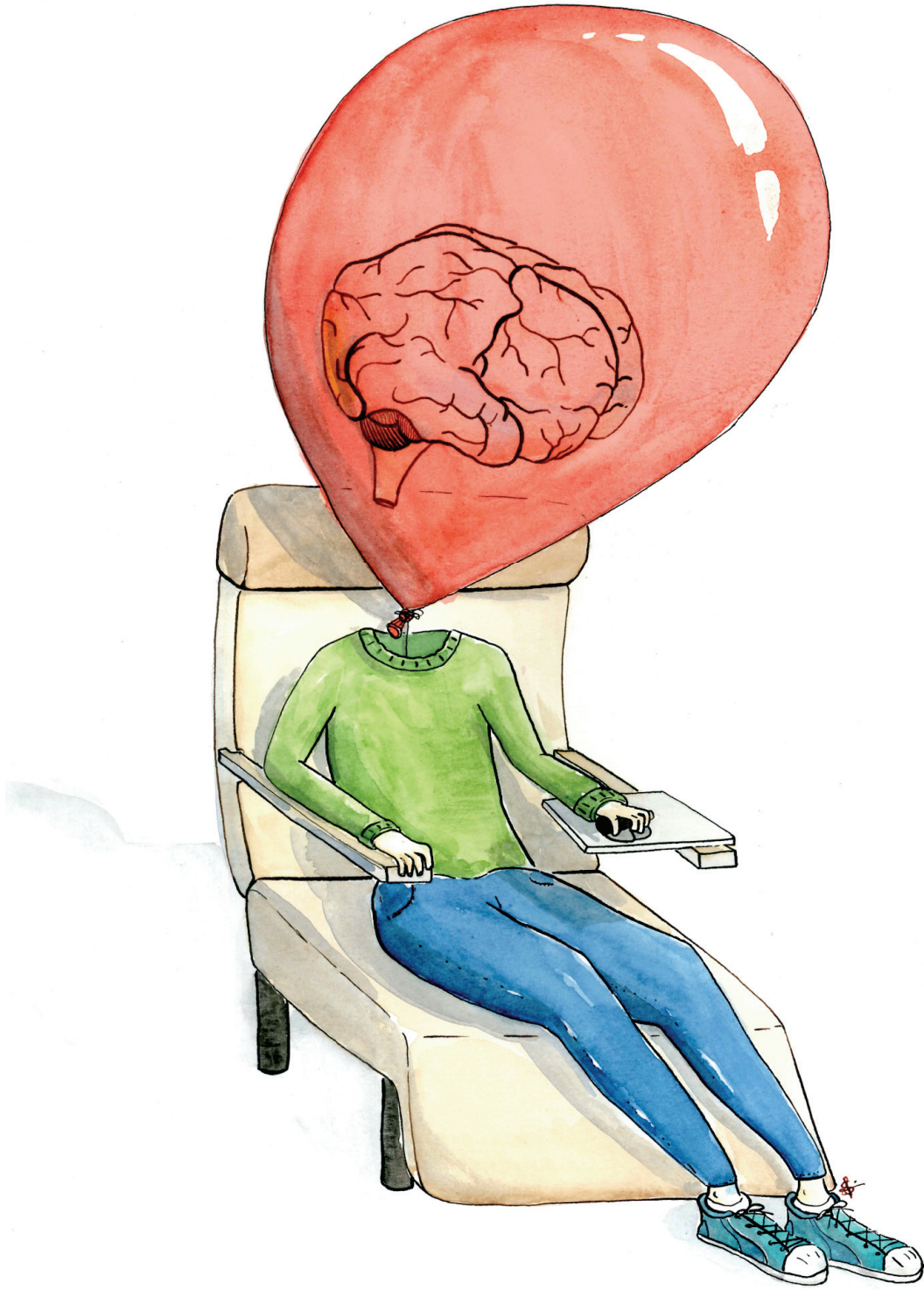
Figure 16 - Induced auditory gamma activity and selective attention. (Left) *Passive listening.* Acoustic stimuli are represented by the black bar, it lasts 50ms and its frequency is 1000Hz. Participants were watching a silent video movie. The average time-frequency power distribution at vertex electrode shows variations in induced gamma activity with respect to the pre-stimulus baseline: an early decrease (red) around 40Hz, 80ms after stimulus onset, followed by an increase (yellow) around 45Hz peaking at 210 and 400ms. (Right) *Active listening:* subjects had to detect 1050Hz rare tones. This distribution shows an early decrease (red) in the temporal area, and a larger central gamma increase (yellow) compared to the passive listening condition, peaking later (300ms) and lasting longer. Auditory induced gamma activity is thus enhanced by selective attention. (from Tallon-Baudry & Bertrand, 1999)

In dichotic listening or active vs passive tasks, this results is confirmed too: induced auditory gamma power is increased for attended versus unattended sounds, see Figure 16 (Fell et al., 2003; Tallon-Baudry, 1999; Tiitinen et al., 1997; Tiitinen et al., 1993). Thanks to electrocortigraphy measures in humans, Ray and colleagues showed that gamma activity is also present in the prefrontal cortex, but only for attended stimuli. The modulation of gamma power begins around 400ms after the onset of the stimulus, and is greater in the high-gamma frequency range (between 80 and 150Hz) (Ray et al., 2008).

Conclusion

In this chapter, we presented a brief overview of the behavioral and cerebral correlates of auditory attention, with a focus on auditory selective attention. We have underlined that attention is a resource-limited process requiring the activation of the frontal network that affects either the thalamus, or the sensory areas.

The similarities between working memory and attention are slowly looming between the two previous sections: they seem to rely on overlapping brain networks and impact several similar brain responses. Furthermore, they might both rely on the creation of neural representation of physical features of the stimuli, a process called encoding. Either selective attention is based on the online comparison with encoded relevant features, or it filters the information to be encoded, whereas working memory's first step is to encode this selected information. In the next section, we will present the current results about attention and memory interactions.



INTERACTION BETWEEN ATTENTION AND WORKING MEMORY

As reviewed in the previous chapters, attention and working memory have been extensively studied. Working memory models describe the encoding of information and its maintenance during a limited amount of time, in a limited-capacity system promoting efficient access, manipulation, and updating. By contrast, selective attention models emphasize the efficient encoding of a relevant target stream despite overwhelming sensory information. If working memory and attention have been studied in an independent way, it appears clearly that modern neuroscience must try to decipher their impact on each other, and to characterize their interaction.

In the model of working memory proposed by Cowan (2004), attention is what allows us to have access to stored information. In Baddeley's model for working memory, the three different information storages are closely related to the central executive, which contains attention processes (Baddeley, 2012). Models of selective attention might have less often incorporated components such as working memory processes.

Looking at the cerebral areas involved during attentional and working memory tasks reveal similitudes between the two types of tasks: as described in the previous sections, they both involve the dorsolateral and ventrolateral areas of the prefrontal cortex, some parietal areas (the posterior parietal cortex, the temporo-parietal junction, the intra-parietal sulcus), and regions specific to the modality involved (frontal eye field, fusiform face area for visual stimuli, but also the medio-temporal lobe for both auditory and visual stimuli).

The following sections will be dedicated to review current knowledge on the characteristics of the interaction between attention and working memory, from psychological to neurophysiological points of view. The majority of studies upon attention and working memory interactions have been led in the visual domain; therefore, we will present the results of these studies and then expose auditory specificities.

A) Impact of Attention on Working Memory

Trying to resolve a complex problem that bothers you, it appears clearly that your phone ringing or pop-ups on your e-mail application that capture your attention will cause you great difficulties. This everyday-life problem is maybe the reason why models have integrated the effect of attention on working memory quite quickly.

1) *Psychological studies in the visual modality*

The main experimental solution to study the impact of attention manipulation on working memory is to present distracting stimuli to the participant while he/she is performing a working memory task. The presentation of these distractors can be announced to the participant who will have to ignore them in favor of the relevant stimuli, but can also be presented without any warning, leading to attention-catching effects. These distractors can be presented during encoding, retention or retrieval steps of working memory tasks, which helps to decipher the impact of attention on each working memory-processing step.

a. Attention manipulation during encoding

In this section, we will review the results enabling to answer the following questions: how does attention impact memory encoding? is attention necessary (and sufficient) to working memory encoding?

(i) How does attention impact memory encoding?

The partial report procedure is a task in which participants have to recall an image in a free narrative way. In the early sixties, it has been shown that it is possible to encode specifically one side of the image, as long as the presented cue, indicating the side of the stimuli to be encoded, persists during the presentation of the image to encode (Averbach & Coriell, 1961; Sperling, 1960). It goes in favor of the hypothesis according to which attention focus impacts which pieces of information are encoded into memory. Working memory has indeed a reduced capacity (Gopher et al., 1996; Luck & Vogel, 1997; Schmidt et al., 2002; Sperling, 1960; Vogel et al., 2001) and top-down control would help to redirect which information, according to their relevance, should be encoded.

Thanks to the comparison of cued versus non-cued trials, it appears that cued information has more chances than non-cued information to be encoded in working memory (Botta et al., 2010; Griffin & Nobre, 2003; Murray et al., 2011; Palmer, 1990; Schmidt et al., 2002). In delayed matching to sample tasks, changes to attended stimuli compared to unattended ones are more often detected (Cohen et al., 2011; Hollingworth, 2004; Irwin & Zelinsky, 2002; Rensink, 1997; Scholl, 2000), therefore the filter applied on primary sensory perception would control the transfer of perceptual representations into visual working memory (Bundesen, 1990; Duncan & Humphreys, 1989; Gordon, 1998).

However, if this selective encoding is effective thanks to cues separating targets from distractors based on their distinct perceptual features (location, color, shape, size, brightness) (Averbach & Coriell, 1961; Banks & Barber, 1977; Sperling, 1960; Turvey & Kravetz, 1970; Von Wright, 1970), selective encoding becomes difficult when more complex distinctive features need to be taken in account, for example alphanumeric cues (distinguishing vowels from consonant, letter from digits, or normal from mirror letters) (Sperling, 1960; Von Wright, 1970). Treisman and colleagues summarize this effect as a physical attribute effect: it is easier to encode selectively one piece of information when its physical attribute(s) rather than its content are different from the rest of the available information (Treisman, 1964).

If attention during encoding selects what is encoded in memory, one can think that it also impacts on the amount of information encoded. However, to our knowledge, there are no studies on the impact of attention manipulation during encoding on working memory span.

(ii) Is attention necessary for working memory encoding?

Thanks to a dual task paradigm combining visual arrays or complex spans and numerical operations presented visually, Shipstead and colleagues (Shipstead et al., 2015) tested several models linking working memory to attention control, and showed that the ability to control and orient attention is a critical aspect for working memory performance. Competitive distracting tasks such as word presentation, forced speeded choice or changing digits reading have negative impacts on recall when they are intricately intertwined with the presentation of the items to be encoded (Barrouillet et al., 2013). In this sense, as performance decreases significantly when attention is driven away, attention would not only orient encoding but would be necessary for encoding (Mack & Rock, 1998). In the same way, display of brief blank fields between alternating displays of an original and a modified scene are not detected (Rensink et al., 1997), implying that there is no storage of a coherent and detailed visual representation of the world in memory

(Noe et al., 2000; O’regan, 1992; Rensink, 2002). The impression of a peripheral world would result in the automatic orientation of attention towards a movement or a change (Rensink, 2002). In a study from Becker and Pashler, participants were presented with 12-digit arrays and had to identify either the highest digit of the array, either the lowest digit not in the array. In a subsequent change-detection tasks, subjects often fail to detect changes that involved the same digits they had previously identified to perform the digit task successfully (Becker & Pashler, 2002). This confirms that visual representations are fragile, volatile. In change-detection tasks, several studies report that the capacity to detect changes is drastically reduced in case of a lack of attention (Mack & Rock, 1998; Rensink, 2002; Simons et al., 2000; Vogel et al., 1998). In particular, some dual-task studies show that an increase of difficulty in the encoding task or in the attention task induce greater dual task interference (Jolicoeur, 1999; Jolicoeur & Dell’Acqua, 1998, 1999; Pashler et al., 2001).

However, the detection of a change in an array of visual items is still above chance for unattended probes (Irwin & Zelinsky, 2002), implying that attention might not be necessary to memory encoding. Several dual-task studies report that modifications in the attentional task does not impact the encoding of a list of spatial locations for example (Blake & Fox, 1969; Pashler, 1991; Pashler et al., 1993; Posner & Boies, 1971).

The main difference between the opposite results presented above during dual tasks remains in the instructions given to the participants. When Pashler and colleagues insist that both tasks are equally important, Jolicoeur and colleagues ask to focus mainly on the attentional task, therefore directing few or many efforts towards resources division respectively. Furthermore, it has been shown that the detrimental effect of the distracting task during encoding on recall performance depends on the pace at which distractors are processed but not on their number, with faster pace resulting in poorer performance (for a review, see Barrouillet et al., 2011).

Finally, these results go in favor of the necessity of visuospatial attention for working memory encoding. The incapacity to detect task-irrelevant items presented in the focus of visuospatial attention reveals that attention is not entirely sufficient for memory encoding (Koivisto et al., 2004; Most et al., 2000; Newby & Rock, 1998).

The elements reviewed in this section allow us to say that attention during encoding might be necessary but not sufficient for working memory encoding. It has a great impact on the selection of the information to be encoded.

b. Attention manipulation during retention

The importance of attention focus during maintenance of information in working memory has been illustrated in many ways. In paradigms using delayed matching-to-sample paradigms with secondary detection tasks during the retention period, top-down attention is voluntarily directed away from the memory task. These paradigms have shown that attention demanding tasks during retention disrupts the working memory process (Brown, 1958; Peterson & Peterson, 1959; Salthouse, 1975; Watkins et al., 1973), whether it is verbal or spatial (Phillips & Christie, 1977; Watkins et al., 1973). Shifts of spatial attention induced by controlled saccades also negatively impact working memory performances (Awh et al., 1998a; Pearson & Sahraie, 2003; Postle et al., 2006; Smyth & Scholey, 1994). However, this effect is reduced for easier working memory tasks: attention is not necessary to single features maintenance but is necessary for feature-conjunction maintenance and for information manipulation (Delvenne & Bruyer, 2004; Wheeler & Treisman, 2002).

It does not require a second task to interfere with memory maintenance: the modulation of involuntary (bottom-up) attention by unexpected salient probes during the retention period also induce an increase of reaction times and a decrease in accuracy to the working memory task (Awh et al., 1998a; Banbury et al., 2001; Jha, 2002; Theeuwes et al., 2009).

However, the opposite effects are observed when task-irrelevant probes share common features (location, identity, for example) with the encoded information their presence, as if in a way, these probes remind to the participant what was encoded (Awh et al., 2000; Awh & Jonides, 2001; Theeuwes et al., 2011). In low memory load conditions, the orienting of spatial attention during retention can create an improvement of working memory performances (Mangun, 1995), but it only works if this orienting is directed towards an encoded feature (Awh et al., 1998a; Awh & Jonides, 2001; Smyth & Scholey, 1994). The highest distracting effects are observed for distractors similar in nature with the encoded stimuli (same type of sounds, or same category of object for a visual display) but with distinct features (location, meaning), their salient effect is higher than with completely different probes (Allen et al., 2012; Klauer & Zhao, 2004; Salthouse, 1975). For visual items such as faces, for example, the presentation of other faces creates great interference. Distracting melodies can be used as distractors for melodies to be encoded, easy-to-ignore if different by timbre or pitch, hard to ignore if highly similar. The presentation of neutral (*i.e.* clearly different from the encoded melody) sounds at the same pace as the encoded melody can help retention.

All these observations led to what was formulated as the attention-based rehearsal hypothesis (Awh et al., 2006; Rensink, 2000, 2002): attention seems to be necessary for rehearsal during the maintenance period. In a more recent study, the presentation of distractors during encoding or retrieval, at different paces, manipulated the retention duration of letters array and prevented their rehearsal, by articulatory suppression effects for example. This study showed that the shorter the retention period is, the more superficial the memory traces are, leading to higher sensitivity to distraction during retrieval (Barrouillet et al., 2013).

c. Attention variation and recall

Presentation of task irrelevant probes during retrieval leads to poorer working memory performance in terms of reaction times and accuracy (Awh et al., 1998a; Banbury et al., 2001; Jha, 2002). Increasing the number of distractors proved to reduce recall performance when intervening tasks are performed at retrieval (Lewandowsky et al., 2008).

However, several studies have also found a positive impact of distractors presentation during retrieval on reaction times, occurring only when these distractors share characteristics with the targets: for example, when a visual uninformative cue is displayed at the location of an item (Awh et al., 2000; Awh & Jonides, 2001; Dowling, 2012; Theeuwes et al., 2011). For example, the display of a visual target at the location of an initial cue containing the necessary information to answer a question such as “was there a red circle?” improves accuracy and reaction time to this question (Nelson & Goodmon, 2003; Theeuwes et al., 2011).

2) *Neurophysiological studies in the visual modality*

fMRI studies showed that voluntary (top-down) attention modulation mediated by informative cues presented before target faces to encode leads to an increased activity of the fusiform face area (FFA) (Zanto et al., 2010). This increase of activity correlates with the degree of connectivity between the FFA and the inferior frontal junction (IFJ), the medio frontal gyrus (MFG), the inferior frontal gyrus (IFG) and the intra-parietal sulcus (IPS). The connectivity between the FFA and the IFJ is correlated with subsequent working memory performances (Bollinger et al., 2010). In this line, a correlation between early modulation by top-down attention of activity in sensory areas and subsequent memorization performances has also been observed in EEG and MEG studies (Gazzaley, 2011; Rutman et al., 2009): participants with larger attentional modulation of the visual P1 amplitude (~100ms post-stimulus presentation) show greater subsequent memory of encoded stimuli.

During maintenance, the brain networks involved in spatial working memory and in spatial selective attention are very similar, with a right-hemispheric dominance of frontal and parietal nodes, confirming the attention-based rehearsal hypothesis (Awh et al., 1998a; Corbetta & Shulman, 2002; LaBar et al., 1999; Smith et al., 1995). However, these similarities come from the comparison of different tasks, different paradigms and conditions. Thanks to a delayed matching-to-sample task experiment involving location memorization, in which orienting cues were presented during the retention period, Postle and colleagues (Postle et al., 2004) revealed that attention orienting during rehearsal induces a baseline shift in areas involved in the processing of the locations to memorize, in particular in the extra striatal areas 18 and 19, in the superior parietal lobule and in the lateralized IPS. The frontal eye field and other frontal areas did not seem to be solicited during this attention-oriented rehearsal. Furthermore, a functional correlation has also been observed by Mayer and colleagues (Mayer et al., 2007), who found common neural substrate for visual working memory and attention: during the retention period, the hemodynamics in the right prefrontal cortex and in bilateral insula increases in an additive fashion for working memory load or attentional search increases.

3) *Impact of attention on working memory in the auditory modality*

Corroborating the results obtained in the visual field, several studies showed that the display of auditory distracting sounds during the maintenance period have a disruptive effect on working memory performances (Colle & Welsh, 1976; Jones & Macken, 1993; Klatte et al., 1995; Neath et al., 1998; Nittono, 1997; Salamé & Baddeley, 1989; Woodhead, 1964). This effect is increased when the physical attributes of the memorized targets and the distractors are close (Banbury et al., 2001), and the presentation of a continuous stream to ignore during the delay period has a smaller impact on working memory task performances compared to an unpredictable changing stream (Tremblay & Jones, 1998).

There have been only very few studies assessing both selective attention and working memory during encoding. Pugh and colleagues, for example, created a dichotic task during which participants had to focus on only one ear during the performance of either a discrimination task with verbal stimuli (ba/da), either a discrimination of ascending or descending pitch variations (Pugh et al., 1996). This pitch discrimination task can be roughly assimilated to a working memory task, in which participants have to remember the first tone in order to tell if the subsequent tone was higher or lower in pitch. Comparing the condition “dichotic listening” to “binaural listening”, they observed an enhancement of the activation of several brain regions, such as the post parietal attention system, superior temporal and inferior frontal areas.

Another study was using tones as targets and distractors in a dichotic pitch classification task to focus on the encoding period. Participants had to ignore distractors that differed in timbre or loudness from the targets (Melara et al., 2005). As the distraction increased (pitch of the distractors closer to the targets), the accuracy in the working memory task decreased, and reaction times increased. The more the distractors were hard to ignore, the higher the amplitude of their associated N1 evoked potential (see Figure 17). This result was interpreted as a decrease of inhibition when distractors are getting closer to the items encoded in working memory, but there is no report of a subsequent impact on working memory encoding-associated EPs (*i.e.* on the target EPs). None of these studies included a manipulation of the difficulty of the working memory task.

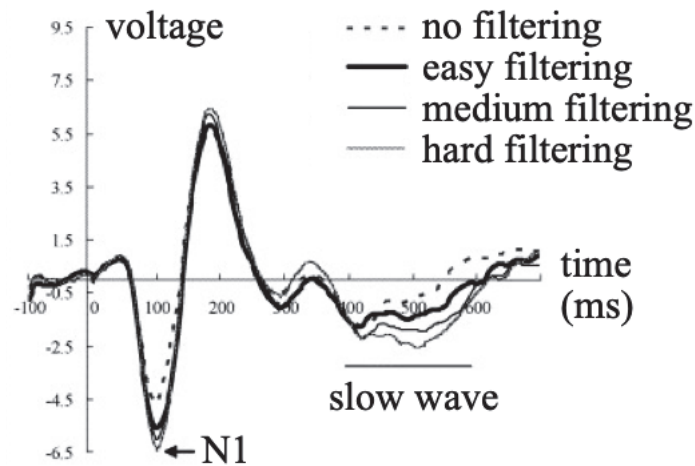


Figure 17 - Effect of selective attention difficulty during a mixed attention and working memory task on the distractors evoked potential. Voltage of the Fz electrode as a function of time. The hardest the distractors are to be ignored, the higher the amplitude of the associated N1 is. In this study, there is no mention of a subsequent effect on working memory associated ERPs. (adapted from Melara et al., 2005)

B) Impact of Working Memory on Attention

The impact of working memory on attention has first been studied in the framework of fluid intelligence: working memory ability was tested as a potential index of performance in various high-level cognitive tasks. Indeed, working memory capacities can predict performance in selection tasks (Vogel et al., 2005). Electrophysiology studies also showed that working memory performance evaluated through different subtests correlates with the amplitude of the visual P100 modulations induced by attention orienting (Fougnie, 2008; Gazzaley, 2011; Rutman et al., 2009).

This framework helped to show that working memory and attention *abilities* are correlated. Here, we will focus on the impact of working memory on attention *processes*.

1) *Psychological studies*

Very few behavioral studies focus on the impact of working memory on attention during the encoding or the recall period. Indeed, it appears quite difficult to evaluate attention orienting thanks to usual attention tasks during these working memory key steps which involve presentation and encoding of the item, or motor response to an attentional task during recall. When searching for an item in a visual array while retaining another item in memory, there is a significant increase of the search time compared to no retention (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006). When the encoded item appears in the search array, it can even facilitate visual search: it is unlikely to be selected for an eye movement, and if the eyes lay upon it, fixation duration is shorter than for other items (Houtkamp & Roelfsema, 2006). The majority of studies about the encoding period report no difference of attentional guidance abilities for different loads to encode (for a review, see Olivers, 2008). One explanation could be that when the targets to look for change for each trial, the resources engaged in memory encoding of the item might not be available for attentional guidance, whatever the memory load is (Soto et al., 2008; Woodman et al., 2007).

On the contrary, the impact of working memory retention on attention tasks during the retention/maintenance period has been intensively investigated. Thanks to various experiments, it has been shown that bottom-up capture during retention is highest if the distracting probes share features with the encoded information (Bacon & Egeth, 1994; Folk et al., 1992; Leber & Egeth, 2006). For example, guiding subjects to look for a specific target feature in a search for a circle among diamond nontargets is disrupted by the presence of a diamond nontarget uniquely colored reveals no distracting effect of this “color” distraction (Bacon & Egeth, 1994). Furthermore, eye-tracking studies show that the encoded stimuli have a significant impact on the direction of the first saccade made during a visual search task (Logan, 1979; Soto et al., 2005, 2008; Soto & Humphreys, 2007), which does not necessarily reduces but rather increases the reaction times associated with this visual search task (Oh & Kim, 2004; Vogel et al., 2001). This goes along with several experiments revealing an increase of attentional capture measured with eye-tracking in visual search when it is performed during a concurrent digit load task (de Fockert, 2001; Lavie et al., 2004; Lepsien et al., 2011).

Visual processing seems to be better at memorized compared to unmemorized locations (Awh et al., 1998a; Awh & Jonides, 2001). Thanks to an innovative experiment, Downing and colleagues (Downing, 2000) showed that attention during rehearsal is guided by the stimulus held in memory. In this experiment, participants had to memorize a face, and after a delay, respond whether or not it was the same face when a second face was presented. During the delay period, they had to realize a target detection task; this target would appear on top on the face encoded in memory or on another face. Performances in terms of reaction times and accuracy were better when the target to detect was presented on the face to remember, revealing increased attention oriented toward this face. Similar results were confirmed by numerous studies (Huang & Pashler, 2007; Olivers et al., 2006; Pratt & Hommel, 2003; Soto et al., 2005).

As irrelevant visual distractors interfere more with visual target detection performance under high working memory load than under low memory load (de Fockert, 2001; Lavie et al., 2004), researchers have proposed that the availability of working memory resources is important for inhibition of task-irrelevant distractors (Lavie, 2005) – see Figure 18. Under low memory load, as formulated by the cognitive load theory, working memory surplus resources could be used to inhibit distractors or facilitate relevant information processing, whereas under high memory load, these resources would not be available and therefore could not be used by attentional processes.

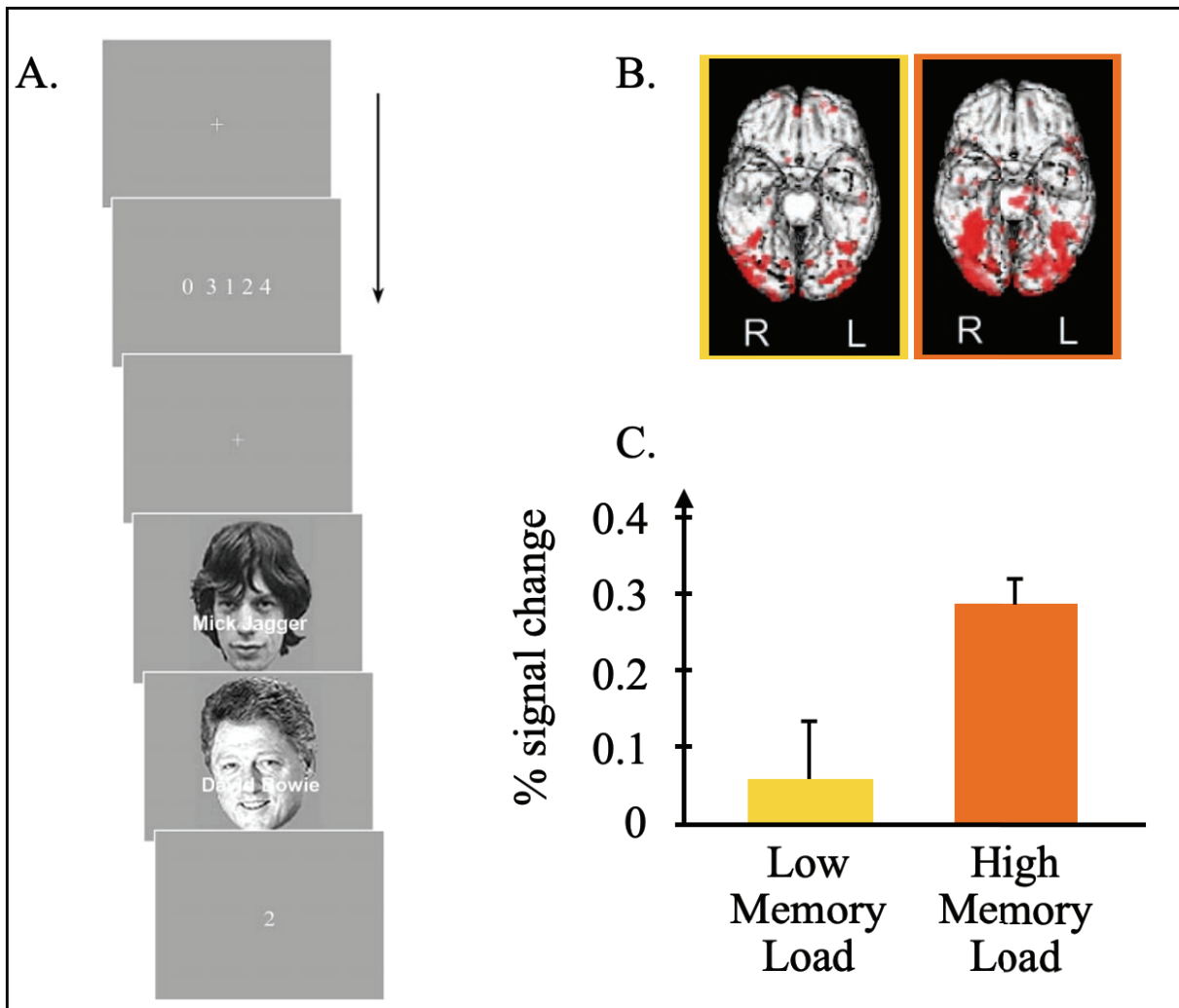


Figure 18 – An illustration of results in favor of the cognitive load theory. *A.* Example of a high working memory load trial with two attention displays. 500ms display of a fixation arrow, then presentation of the memory set (1500ms). Under low memory load, the digits are always in the order 0,1,2,3,4. After the memory set and an 850ms long display fixation cross, two to four attention displays are presented (500ms each+ 1250ms-blank response interval). After the final attention display, a memory probe is presented for 3000ms, participants had to report which number is following the probe in the initial array (here, the answer is “4”). *B.* Two views of the ventral surface of the template used, with superimposition of the loci with significantly greater activity in the presence compared to absence of distractor faces under conditions of low (left, yellow) or high (right, orange) working memory load. *C.* Mean of the distractor-related activity (percent signal change for face presence minus face absence) or the maxima of the interaction in the right fusiform gyrus (36, – 64, –16), plotted separately for low and high working memory load. Data are averaged across participants. Error bars represent inter-participant standard error. (adapted from Lavie, 2005)

2) *Neurophysiological studies*

Electrophysiology is a great tool to study the impact of working memory encoding on attention. It has indeed been shown that the presentation of probes with relevant features during encoding induces changes in the neuronal activity, implying that one object “wins” the focus of attention compared to another one. This phenomenon has been named as the biased-competition model of visual selection (Desimone & Duncan, 1995). This has been confirmed by observations of sustained activation in prefrontal regions and posterior regions when distractors sharing features with the target to be encoded are presented (Desimone, 1996). The use of location cues to be retained revealed that the activation of the frontal network involved in attention orienting and selection is interconnected with the working memory neural correlates (Corbetta et al., 2002).

Several fMRI and ERP studies showed that rehearsal in working memory modulates early processing in visual areas associated to the memorized spatial locations (Awh et al., 1998b, 2000; Jha, 2002; Munneke et al., 2010). Furthermore, inferior temporal and prefrontal cortex target-specific neurons still fire during retention, which is interpreted as a neural marker of working memory induced attention guidance (Chelazzi et al., 1993, 1995; Downing, 2000; Duncan & Humphreys, 1989).

3) *Impact of working memory on attention in the auditory modality*

In the auditory domain as well, correlations between working memory capacity and selective attention performance have been reported. With working memory and attention evaluated in separate tasks, it appears that participants with lower working memory capacity (WMC) are more likely to notice their name in the unattended stream of a dichotic task (Beaman, 2004; Conway et al., 2001). More recent investigations using non-verbal stimuli showed that participants with higher WMC show smaller N1 ERP response to distractors, thus revealing better performances at preventing processing of irrelevant stimuli (Sörqvist et al., 2012; Tsuchida et al., 2012). Therefore, it appears that WMC are negatively correlated with involuntary attention, but positively correlated with voluntary attention.

The most common way to test the impact of working memory on attention is to impose the performance of an attentional task during the retention period. In a task involving continuous white noise bursts as targets and pulsed bursts of noise as distractors during the maintenance period of a visual digit recall task, Dalton and colleagues showed an increase of interference from the distractors, *i.e.* decreased performance in the memory task, under high memory loads (Dalton et al., 2009). Similar results were found by Sabri and colleagues, who also investigated brain activity: they observed a linear increase in the auditory cortex BOLD response, and a linear increase in ERPs between 130 and 230ms post- irrelevant stimulus, for increased perceptual demand (Sabri et al., 2006, 2014). Thanks to a combination of a n-back task (n=1 or n=2 corresponding to low and high memory load) in one ear and a selective attention task with task-irrelevant speech sounds in the other ear, they also confirmed the observation of larger neural responses for irrelevant sounds (see Figure 19) and decreased selective attention performance under higher memory loads (Sabri et al., 2014). This decrease in performance could be explained by an increased latency of the inhibitory component to distractors under high load, while the facilitatory component to relevant sounds seems unaffected by memory load (Bidet-Caulet et al., 2010).

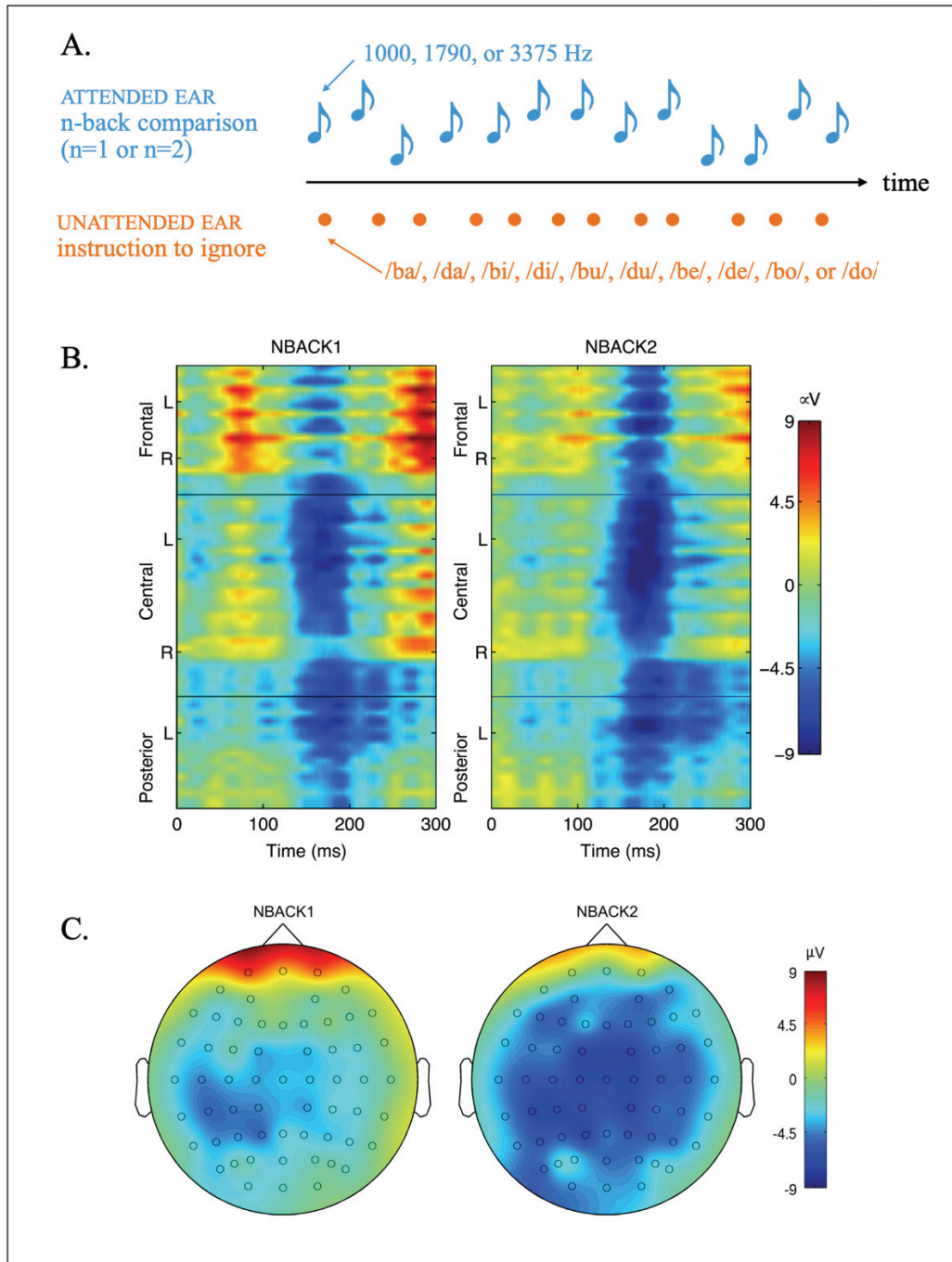


Figure 19 - Effect of working memory load on the activity linked to distractors. *A.* Task presentation: *n*-back task on the attended ear in which tones are presented at a regular rhythm (*n*=1 or *n*=2 implying low or high memory load), dichotic listening and instruction to ignore the distracting syllables displayed in the other ear, never overlapping the attended tones. *B.* Spatiotemporal maps from 60 EEG electrodes: grand average ERPs of irrelevant syllables at each electrode as a function of memory load (NBACK1 and NBACK2 refers to *n*-back tasks with *n*=1 and *n*=2 respectively, thus inducing low and high memory loads respectively). The y-axis represents the frontal, central, and posterior electrodes. Each group of electrodes (frontal, central, posterior) is arranged top to bottom according to their lateral position from left (L) to right (R), with the midline electrode in the middle. *C.* Zoom on the N1 time window: mean scalp distribution for irrelevant syllables in the 130-210ms time window, in NBACK1 and NBACK2. In both panels, the color scale represents the amplitude in μV . The interaction between memory load and irrelevant information processing reveals stronger activations in frontal and parietal areas in the N1 time-range in case of a higher memory load. (adapted from Sabri et al., 2014)

As in the visual modality, there is some contradictory evidence to these results, finding that increasing working memory load would reduce distraction (SanMiguel et al., 2008). More precisely, it has been shown that the variation of interference caused by different levels of distractors is reduced for high working memory loads (Berti & Schröger, 2003; Muller-Gass & Schröger, 2007). However, these results come from studies where targets and distractors were not distinct: the distracting features were presented as part of the attended target stimulus. Another parameter to take into account would be the degree of resemblance between targets and distractors: the more features they share, the higher is the distraction (Dittrich & Stahl, 2012).

All these elements could be explained by the cognitive load theory presented earlier (Lavie, 2005). To our knowledge, there is no study combining working memory effect on attention during encoding using similar distractors and targets, and different levels of distraction and different levels of load, allowing to precise how auditory attention and working memory fits into the cognitive load theory, which has been elaborated from visual investigations. Most importantly, all these auditory studies focus on the impact of memory load on attentional processes during the maintenance of the information. Therefore, there is a lack of information about how working memory encoding and retrieval impacts attention selection and vice-versa.



GENERAL OBJECTIVE OF THE THESIS

In our everyday lives, we are constantly juggling with different tasks and information flows, both external and internal. We select the relevant stream of information and try to ignore irrelevant distracting information (selective attention) in order to memorize and/or manipulate some pieces of information (working memory). Both selective attention and working memory are supported by of the dynamic activation of prefrontal and temporal networks (reflected in rapid or sustained event-related responses, evoked or induced oscillatory state of the brain at different frequencies).

Several points can be raised regarding the literature about the interaction between selective attention and working memory. **First**, the auditory domain has been much less investigated than the visual domain. However, there is a rich representation of the auditory modality in the prefrontal cortex (see the first Chapter) which could be the substrate of this interaction. Furthermore, because auditory perception is not spatio-topic, and because auditory information is transient by essence, auditory information always needs to be selectively processed. **Second**, when focusing on the auditory modality, most research conducted on the interaction between attention and memory was either mixing modalities, or mixing verbal and non-verbal items, or even both. Even if it is interesting to mix different kinds of materials, there is a lack of investigation using only non-verbal auditory stimuli. Using non-verbal stimuli is very useful to reduce interference from language processing, in particular for further developmental studies. **Third**, experiments manipulating attention orientation during the auditory memory retention period outnumber by far the attention manipulations occurring during auditory memory encoding. However, working memory encoding is a necessary step and the creation of memory traces is at least as important as its refreshment and has been shown to be related to attentional status in the visual modality. **Finally**, the majority of the results on attention and working memory interaction comes from paradigms manipulating the difficulty of one of the two processes and see its impact on the other one, without measuring the opposite effect. Therefore, knowledge about the interaction is, for the most part, built from one-way pieces.

This PhD work thus aims to test and characterize the interaction between selective attention and working memory processes during the encoding step of working memory, in the auditory non-verbal domain. To this end, we designed a new paradigm allowing to manipulate both selective attention and working memory during encoding in an independent way, thanks to non-verbal auditory stimuli. The design arguments for this new paradigm are presented in the following section (MEMAT: THE DESIGN OF A NEW PARADIGM).

We first tested this new paradigm in non-musician healthy young adults. We also adapted the paradigm to test a specific hypothesis about load theories of attention. We tested the paradigm on a population with increased working memory capacities in the auditory modality: professional musicians. These investigations and their associated findings led to the redaction and submission of an article presented in the first section of the results.

As we studied the impact of enhanced working memory abilities (in musicians) on the interaction between attention and working memory, we chose to create a mirror situation in which we would analyze the impact of different attentional profiles on MEMAT performances. To this aim, we compared behavioral (and electrophysiological, non-presented) responses of low- and high- frequency dream recallers, which are known to exhibit different attentional profiles (Eichenlaub et al., 2014; Ruby et al., 2013). This investigation and its associated findings are presented and discussed in the second section of the results.

Finally, this paradigm was designed to be used in electrophysiology experiments. Using Magneto-Encephalography (MEG) recordings, we characterized attention and working memory, as well as their interaction during encoding thanks to the study of oscillations and event-related responses/fields (ERs). These investigations and their associated findings are presented and discussed in the third section of the results.

MEMAT: THE DESIGN OF A NEW PARADIGM

MEMAT paradigm (for MEMory and ATtention) aims to test the interaction of selective attention and working memory processes during memory encoding in the auditory modality.

In order to reduce the impact of language processing on task performance, we used non-verbal stimuli. This would be useful for further studies in children, and more generally for all kind of participants with language disorders. There are multiple possibilities for non-verbal sounds: white noises, environmental sounds, instrumental sounds, synthetic tones, etc. For more simplicity, we chose to use synthetic tones with eight harmonics. Music is universal and such music-like stimuli could allow to test participants with different cultures. As musical tones were chosen, the simplest way to implement potential melodies was to restrict ourselves to the western C scale, with no alterations of the tones. This choice also reduces the chances of creating melodies more salient than others. The ambitus of the sounds (*i.e.* the range between the lowest and the highest tones) was delimited according to melody creation necessities, *i.e.* to the possibility to create enough melodies following the rules we established (see below) (from 110 to 440 Hz for the behavioral experiment, from 65 to 1046Hz for the MEG experiment, see Figure 22).

Once the nature of the stimuli chosen, the first steps were to choose which tasks would be used, and how attention and memory could be manipulated in an independent way.

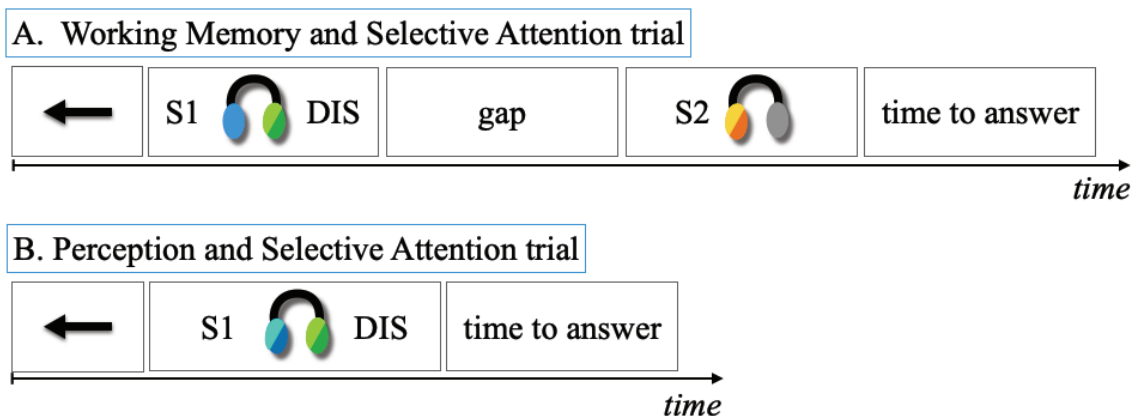


Figure 20 - Brief description of the trials for the Working Memory and Selective Attention task (A.) and the Perception and Selective attention task (B.). The melody to target (S1) is presented in one ear (blue) while an easy- (light green) or hard-to-ignore (dark green) distracting melody is played in the other ear. In the working memory and selective attention trials (A.), a melody (S2) to compare to the melody encoded previously is presented after a gap. the difference to detect if any can be easy (yellow) or hard (orange) to detect. In the perception and selective attention trials (B.), the goal is to say whether the two last tones of the target (S1) are identical or different, the discrimination task can be easy (light blue) hard (dark blue).

There are several existing tasks to test working memory performances, which were presented in previous sections of the introduction. In the case of non-verbal stimuli, free recall of a succession of tones would add difficulties of production and is therefore inappropriate. Delayed comparison between several sequences of tones and one reference sequence has not been very much used, as the presentation of several new auditory sequences cannot be simultaneous, and the succession of presentation of new sequences increases the retention period for each new sequence presented. What seemed to be an appropriate paradigm to measure auditory non-verbal working memory is the delayed matching to sample test. In this task, participants would hear a reference sequence of tones; after a delay, a second sound sequence would be presented (see Figure 20). Participants have then to answer the question “were these two melodies identical or different?”. The use of buttons to answer facilitates the automatization of the data analysis and allows to measure precise response times.

In a scientific paradigm, to study the effect of a process, one must compare two conditions in which this process is differently implicated. One possibility, in our case, could have been to create one condition with the previously described working memory task, and another condition in which participants would not have to memorize the reference melody. We created a condition without memorization but with a goal, a perception task. We also chose to create two levels of difficulty of the memory task. Indeed, we wanted not only to find evidences for attention and memory interaction, but also to characterize it. Therefore, the control condition for the memory task is an easier condition, in which working memory processes are still involved. In order to create two difficulty levels, we played on the memory load: the harder it is to catch the difference between the new and the reference sequence, the more precisely the reference sequence must be memorized. Therefore, there would be blocks for which we would tell participants that the memorization would be harder than others, thus requesting them to put more effort in the memorization.

But how do we make differences between two melodies harder to spot? The simplest way would be to make the array longer, i.e. create longer melodies. However, this would induce bias for changes occurring at the beginning or at the end of the melody, and create differences between sequences of different conditions, which is not compatible with electrophysiology recordings, therefore we did not choose this option and chose to create only 4-tone long melodies: four non-verbal items seemed to be an appropriate working capacity use. Several studies showed that it is easier to perceive changes that break the harmony rules of the melody, wider changes, or

changes impacting the contour of the melody (i.e. changing the ascending/descending pattern of the melody) (Caclin & Tillmann, 2018; Dowling, 1999; Dowling, 1978; Schulze et al., 2012; Schulze & Tillmann, 2013). As we chose to use C-major scale tones, we focused on the two last parameters. The second sequence could be different from the first sequence by one tone only, and on the second, third or fourth note. In the low memory load condition (see Figure 21 – A. and D.), a change in the to-be compared melody would be of 5 or 6 semi-tones and would change the contour of the melody. In the high memory load condition (see Figure 21 – A. and D.) a change in the to-be compared melody would be of 3 to 4 semi-tones and would not induce a change of the melody contour.

This working memory task had to be combined with an independent selective attention manipulation during encoding. As presented in the main introduction (see

AUDITORY SELECTIVE ATTENTION), the historical and easy-to-use task to manipulate selective attention is the dichotic listening paradigm. In this task, participants have to focus on only one ear, which can be previously indicated by a cue, while distracting sounds are played in the other ear.

One of our goals was that the targets and the distractor sounds would be acoustically matched, so that the only difference between them would be the allocation of attention (attended vs. ignored, see Figure 20). Therefore, the distracting sounds are similar to the targets, *i.e.* melodies of synthetic tones (see Figure 21). One created melody was used as many times as a target melody or a distracting melody across blocks and participants.

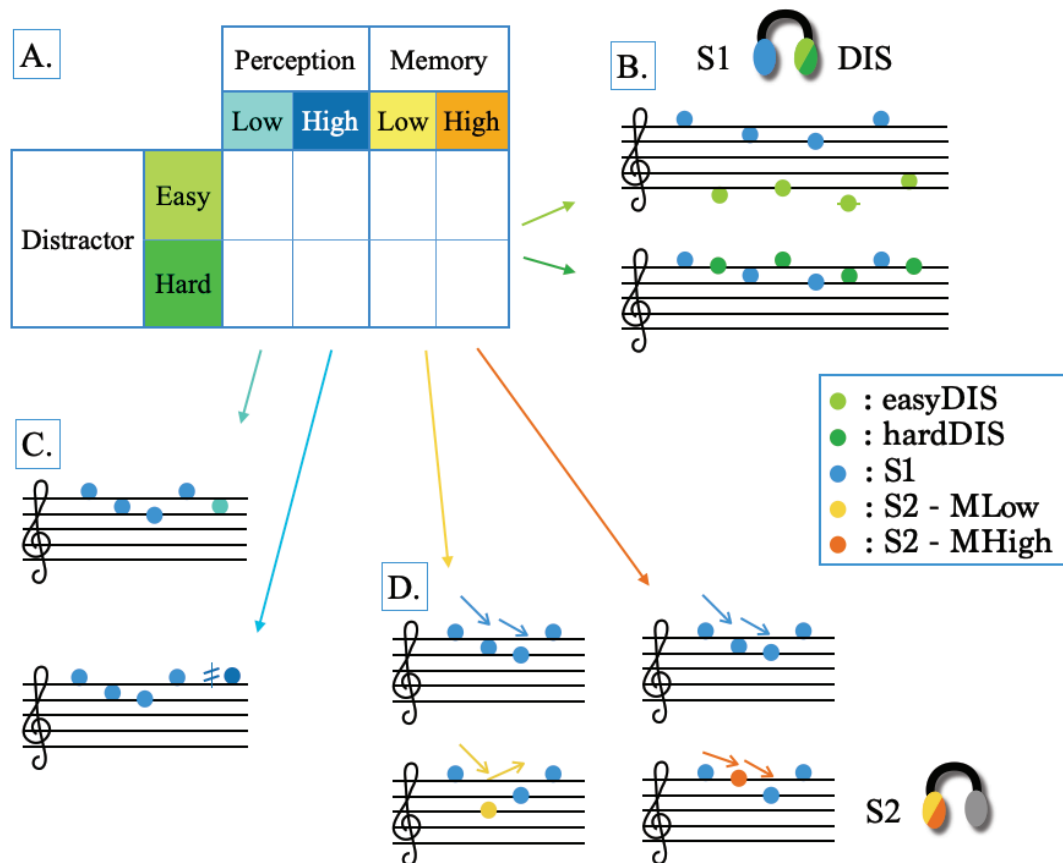


Figure 21 - Parameters of task difficulties. *A.* Overall view of the different conditions. *B.* Description of the different distractor difficulty levels. A melody is an easy distractor when its frequency range is 6 to 7 semi-tones apart from the associated S1 frequency range. Hard-to-ignore distractors are composed of tones of the same frequency range as their associated S1 melody. *C.* Description of the Perception task difficulties. The two last tones to compare are different from 3 to 4 semi-tones (ascendant or descendant) in the low-difficulty perception condition, whereas they differ from 1 quarter of a tone (ascendant or descendant) in the high-difficulty perception condition. *D.* Description of the Memory task difficulties. In the low memory load condition, the difference to catch between S1 and S2, when present, can be on the second, third or fourth tone, is an interval or 5 to 6 semitones, and creates a contour variation. In the high memory load condition, there is no contour variation induced by a change in S2, and the interval of change is of 1 to 2 semi-tones.

In the dichotic listening paradigm, sound presentation rhythm could be randomized, inducing eventual overlap of the sound in the two ears. However, random presentation of sounds induces rhythm effects, and rhythm perception is a complex process which could interfere with pitch perception. Furthermore, pilot testing showed that the simultaneous presentation of the melodies in the two ears would create too much interference and would make the task too hard to perform. Hence, we chose to present target and distracting melodies at the same rate, in an interleaved fashion (see Figure 21 - B). Melodies are constituted of 250ms long tones. The target and the distractors are nested: the 250ms long tones were presented in the different ears one after another, with an onset-to-onset time interval of 500ms for each melody taken apart, but with no gap between the tones if considered together (see Figure 22).

As for the working memory task, we chose to create two levels of difficulty for the selective attention manipulation. To this aim, we designed two levels of distractibility of the distracting melodies. As it has been shown that the more similar the targets and the distractors, the harder selective attention (Woods et al., 2001), our easy-to-ignore distracting melodies (see Figure 21 – A. and B.) are composed of tones that are in a lower or higher frequency range compared to the tones of the targets. In the hard-to-ignore condition (see Figure 21 **Erreur ! Source du renvoi introuvable.** – A. and B.), the tones of the targets and of the distractors belong to the same frequency range.

In the first steps of the construction of our paradigm, we decided to create a separate control task in which we could see the impact of the attention manipulation on a perception task. In the case of an absence of difference between the low and high memory loads, this separate task would create an independent control for the interpretation of the results. In this task, we did not want working memory to be involved, but still wanted to manipulate selective attention. Therefore, we kept the dichotic listening frame, but this time, participants did not have to memorize the melody. In the perception task, they would rather compare the two last tones of the melody presented in the ear of interest (S1). To keep the structure of the combined working memory and attention task, two levels of difficulty were created for the perception task (see Figure 21– A. and C.).

With the tasks defined more precisely, and the different conditions raising more clearly, several details were submitted to reflection. In particular, the design of the melodies and their balance across trials and participants have been submitted to several rules.

The wider interval between two tones of a given melody is 7 semi-tones (this interval is not always present in one melody; it is the maximum range it can reach). For diversity and lack of redundancy, two subsequent tones cannot be identical, the number of repetitions in the melody is maximum one (there cannot be two tones repeated one time each, for example), and a given melody should contain at least one ascending interval and one descending interval (see

Figure 22). Given the ambitus of the stimuli, we chose several intervals in which melodies were created (see

Figure 22). The same number of melodies was created for each given interval.

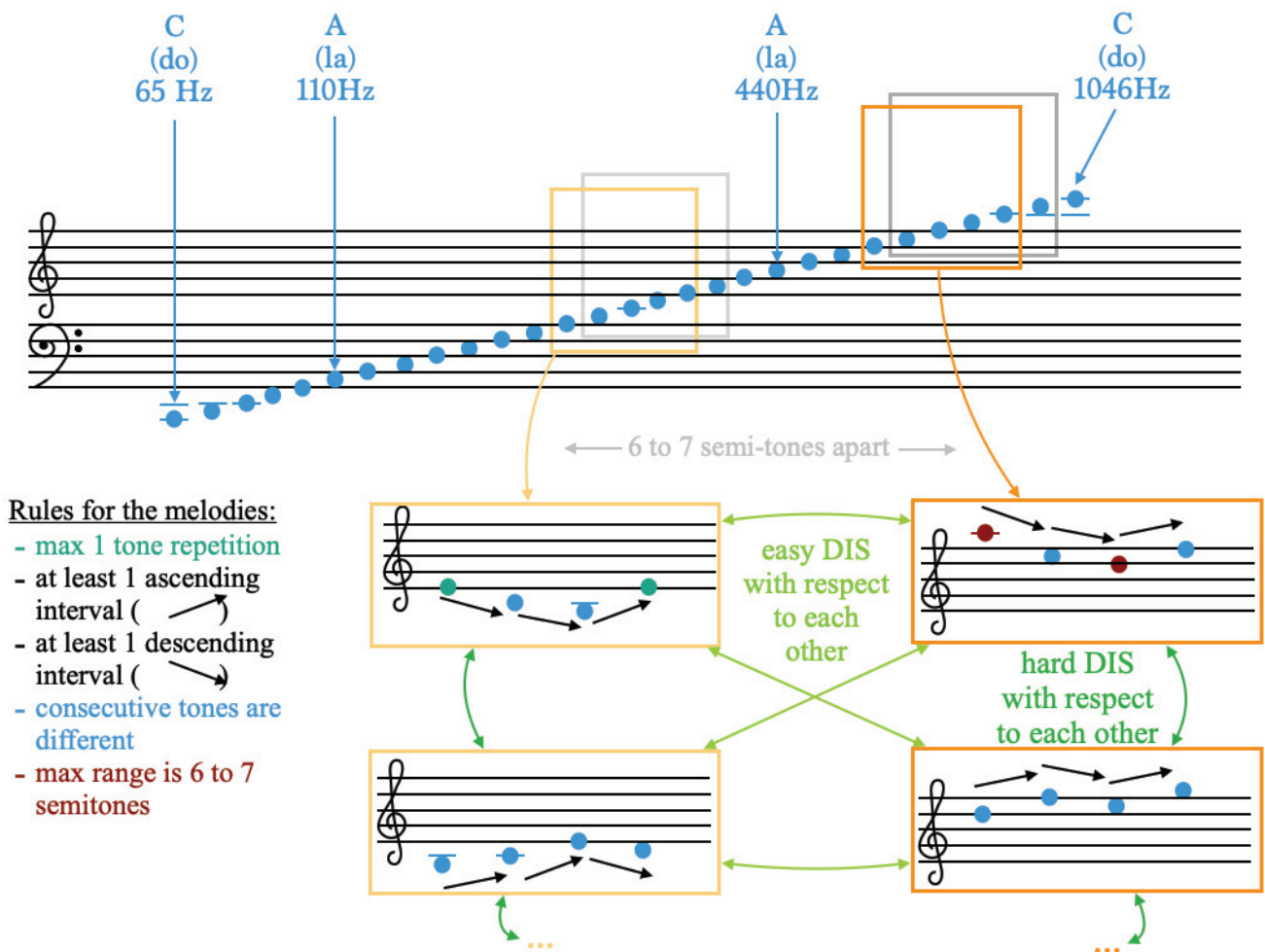


Figure 22 – description of the stimuli. The ambitus (up panel) of the behavioral (110 to 440Hz) and MEG (65 to 1046 Hz) experiments. As represented by the frames, intervals for easy distraction are 6 to 7 semi-tones apart: a melody taken in the orange frame, for example, can be an easy-to-ignore distracting melody for one melody created with the tones delimited by the yellow frame (indicated by the light green arrows). Two melodies created with the tones belonging to the same frame or interval can be associated in the hard-to-ignore distractors condition (indicated by the dark green arrows). Such

frames were defined for the entire ambitus of the stimuli. Generated melodies follow several rules (down panel) illustrated by examples.

From the beginning, the MEMAT paradigm was constructed to be adapted for electrophysiological recordings. This was important for the choice of the stimuli but has also been of great importance for the design of melodies.

In order to cancel potential effects of specific melodies, such as salience (which can impact the difficulty of the selective attention task), or greater pitch variation effects (which can impact the working memory task) for example, we created a simple rule with numerous consequences: one melody should always be used in every condition. This means that a given melody plays the same number of times the role of a target melody in the low or high memory load, the role of an easy distractor and the role of a hard distractor. Indeed, the difficulty of the distractor only depends on the target to which it is associated. It also implies that the side of presentation is the same number of times left and right for a given melody, whatever its status is. For each participant, a given melody is used once by crossed condition, *i.e.* once in the low memory load – easyDIS, once in the high memory load – easyDIS, etc.

In order to cancel stimulus-response association, we controlled the association of one melody to a given answer: for a given melody, whether it is a target or a distractor, the associated answer is “identical” as many times as “different”.

GENERAL HYPOTHESES

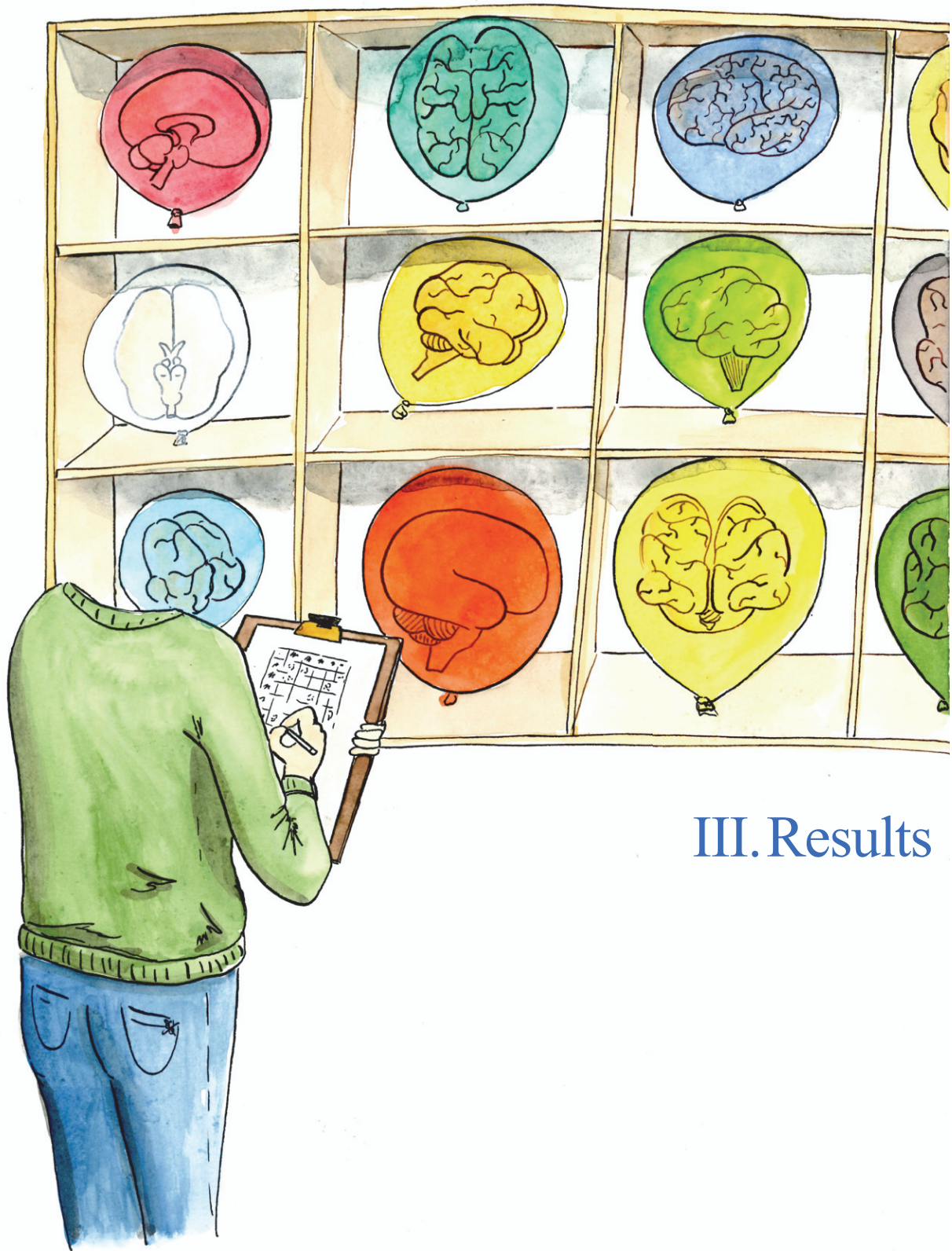
On the behavioral level, we expect longer reaction times and a larger amount of errors in the high compared to low memory load condition, in the high compared to low perception load condition, and in the hard- compared to easy-to-ignore distractors condition.

We are aiming to study an interaction between attention and memory. Therefore, we expect different impact distractors difficulty according to the memory load conditions, an interaction that could be different for the different perception load conditions.

This interaction could be observed in many ways. If selective attention and working memory share cognitive resources, there should be more difficulties to inhibit the distractors under high compared to memory load, and even more when the distractors are hard to ignore. If selective attention and working memory share perceptual resources, a high working memory load could recruit perceptual resources, making it impossible to perceptually process distractors. If the task happens to be really hard under high memory load, there could be an absence of difference between easy and hard to ignore distractors, as they either all become very hard to ignore, or are not even processed because there are no more resources left for them. If the task happens to be quite easy under low memory load, there could be an absence of difference between the different types of distracting conditions, as all distractors could become quite easy to ignore.

According to the literature, musicians should show better working memory performances than non-musicians. In the same way, we expect high dream recallers to have poorer attentional performances than low dream recallers. This effect should impact the interaction between attention and working memory condition. One could expect that, if working memory and selective attention share cognitive resources, facilitation of one process by natural capacities should allow resources to be directed to the other process, therefore creating less differences between difficulty levels.

In electrophysiological recordings (MEG), we expect evoked responses (P50, N1) to distractors to be reduced in comparison with targets, reflecting inhibition of the irrelevant sounds and facilitation of the relevant sounds. This difference should be reduced for hard-to-ignore distractors, as they would be less correctly inhibited. We expect this reduction to follow the pattern observed in the behavioral measures. Sustained responses amplitudes should be lower for low versus high memory load, and lower for easy compared to hard to ignore distractors. We expect the power of auditory alpha oscillations to follow the interaction present in the behavioral responses in the auditory cortex. The modulation of oscillatory activities in the frontal cortex could allow us to assess the central monitoring of selective attention and working memory processes, for resource allocation.



III. Results

**SHARED COGNITIVE RESOURCES BETWEEN MEMORY AND ATTENTION DURING
SOUND SEQUENCE ENCODING**

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Highlights

- Attentional filtering and memory load were manipulated during sound sequence encoding
- Both manipulations impede on performance in a recognition task with short melodies
- Musical training is associated with better memory but not attention skills
- Cognitive resources are shared between auditory attention and working memory
- Attentional filtering and memory encoding appear as only partly separate processes

Abstract

Attention and memory are two essential processes interacting during cognitive processing of environmental information. However, their interaction is not yet well characterized in the non-verbal-auditory domain, especially during memory encoding. We independently manipulated both of these processes in a Delayed-Matching-to-Sample of two series of tones, played successively in one ear. During the first melody presentation (encoding), weakly or highly distracting melodies were played in the other ear. The difference to detect between the two melodies to compare could be easy or difficult, requiring low or high memory load. We tested this paradigm in 16 non-musician and 16 musician participants. All participants were less accurate under high memory load and difficult-to-ignore distractors, validating the paradigm design. Furthermore, there was an interaction between memory load and distractor difficulty, speaking for shared resources between working memory and attention. Non-musicians showed less difference between easy and difficult-to-ignore distractors under higher memory load; while musicians, showing better performance than non-musicians, presented less difference between easy and difficult-to-ignore distractors under low memory load. Thanks to a second experiment including trials without distractors, we could determine that the reduced distractor difficulty effect under high memory load in non-musicians was due to a cognitive load increase resulting in a reduced filtering out of both weakly and highly distractors.

Overall, we conclude that working memory and selective attention interact via shared cognitive resources during sound sequence encoding, in line with the cognitive load theory.

Keywords

Attentional filtering; Working Memory; Auditory; Non-verbal; Memory encoding; Selective Attention

Introduction

Attention and working memory are two essential cognitive processes. If attention has been defined in many different ways for the past decades, we refer here to the ability to allocate resources to processes, these resources being limited. For example, attention is the process that allows you to focus on this article and not on the noise that surrounds you. In particular, selective attention is crucial for selecting relevant information and filtering out distracting elements. To which extent task-irrelevant stimuli are processed is at the heart of a longstanding debate between early and late-selection theories of attention (Driver, 2001). According to the early selection models (Broadbent, 1957; Treisman, 1960), there is an attenuation of the sensory processing of non-relevant information. According to the late selection model, irrelevant events are fully processed at the sensory level, but less accessible to higher cognitive functions such as memory or consciousness (Deutsch & Deutsch, 1963; Posner, 1980). Several electrophysiological experiments have shown that processing of irrelevant sounds can be reduced as early as the first cortical processing stages (Bidet-Caulet et al., 2007; Chao & Knight, 1998; Knight et al., 1999). Importantly, gating of irrelevant information seems to depend on the resources necessary to process relevant information: distractor processing can be reduced at early stages when processing of task-relevant stimuli involves high perceptual load (*i.e.* high amount of perceptual capacities are devoted to relevant information processing), while under low perceptual load distractor processing would be reduced at later processing stages (Cartwright-Finch & Lavie, 2007; Forster & Lavie, 2007; Handy & Mangun, 2000; Huang-Pollock et al., 2002; Lavie, 1995; Lavie et al., 2014; Lavie & Cox, 1997; Lavie & Tsai, 1994). This late selection has been shown to be highly impacted by the amount of available cognitive resources, which depends on the cognitive load of the task at hand (*i.e.* amount of cognitive and executive processes required to perform the task) (Lavie et al., 2004; Lavie, 2005; Yi et al., 2004).

Working memory (WM), on the other side, is the cognitive ability to maintain and manipulate information during a limited period of time (Baddeley, 1992; Joseph et al., 2016). It allows you to understand what is written here, as you can keep in mind the previous sentence while reading this one and relate them together. Information, while accessible, is transcribed in the brain as memory traces: this process is called encoding. Memory traces are refreshed during the retention period in which information is no longer reachable; when needed, memory traces are re-activated during retrieval (Baddeley, 1992). In Baddeley's influential WM model (Baddeley, 2000; Baddeley & Hitch, 1974), working memory is a multi-component system, including

active storage components (phonological loop and visuo-spatial sketchpad) and a central executive system which is regarded as an attentional control system. As reviewed in Adams et al. (2018), most models of working memory acknowledge a role for attention in storage and/or processing of the information held in working memory.

Attention and WM have been studied separately for a long time but more and more research projects in modern psychology and neuroscience try to decipher their impact on each other, to uncover their common resources and to characterize their cooperation (Awh & Jonides, 2001; Colflesh & Conway, 2007; Rutman et al., 2009).

In the visual domain, several studies have investigated the impact of attention on each memory step. It appears that presenting irrelevant images or symbols during encoding leads to lower recall performance, underlining an influence of selective attention on WM capacities. Regarding early sensory processing stages, distractors-related modulation of the P100 event-related potential and WM performance are directly correlated (Fougnie, 2008; Gazzaley, 2011; Rutman et al., 2009). During memory retention and retrieval, presentation of task-irrelevant probes can enhance performance in terms of reaction time, accuracy and span if they share features with the encoded information (Awh et al., 2000; Awh & Jonides, 2001; Jay Dowling, 2012; Theeuwes et al., 2011), but otherwise tends to reduce performance in terms of reaction time and accuracy (Awh et al., 1998; Banbury et al., 2001; Jha, 2002), interrupting memory traces update (Postle et al., 2004; Soto et al., 2008). During the retrieval period, unexpected probes can reduce recall performances (Park et al., 1989), but attention orienting probes can help to recall more features or items (Nelson & Goodman, 2003). In the auditory domain, most studies have been conducted using verbal stimuli, revealing that divided attention during encoding impedes recognition of words assigned with a high value in the experiment design (Elliott & Brewer, 2019), and divided attention during retrieval causes performance drop (Lozito & Mulligan, 2006). In the auditory domain, most studies focus on the impact of distraction during the retention period, showing evidence for a major impact of attention on selection, span and update of encoded information (for a review, see Banbury et al., 2001): more numerous distractors lead to poorer performance.

Concerning the effect of WM on attention processes, studies with auditory stimuli have shown that distraction effects (Berti & Schröger, 2003; SanMiguel et al., 2010) and the inhibitory component of attention are reduced under high memory load (Bidet-Caulet, Mikyska, & Knight, 2010). Whatever the modality tested, performance in attention tasks is poorer under high memory load (Awh & Jonides, 2001; Colflesh & Conway, 2007; Lavie, 2005; Melara et al.,

2005; Pratt et al., 2011), except when relevant features are part of the memorized information (J. S. Johnson et al., 2007).

Overall, these results suggest that there is an overlap, at least partial, between selective attention and WM processes. The aim of the present study is to uncover the links between non-verbal auditory attention and WM during encoding: how do they interact? Focusing on non-verbal auditory stimuli allows us to evaluate attention and memory in the absence of language-dependent processes.

Few studies have investigated the impact of attention during memory encoding. In the visual modality, attention impacts span and selection of the encoded information (Fougnie, 2008; Gazzaley, 2011), but to the best of our knowledge, the interaction between attention and memory during encoding has not been explored in the auditory domain for non-verbal stimuli. In the present study, we propose a novel paradigm to manipulate both non-verbal auditory attention and WM during sound sequence encoding, allowing us to study their respective impact on each other. To this aim, we design delayed-matching-to-sample tasks where participants have to compare two sequences of sounds (short isochronous melodies) played subsequently in the same ear. The presentation of the first melody is coupled with the presentation of a distracting melody in the other ear. The differences between the melodies to compare can be either easy or difficult to detect, inducing low or high memory load.

Additionally, we create matched Perception tasks where participants have to compare the last two tones of a melody played in one ear, in the presence of a distracting melody in the other ear, under high or low perceptual load (difficulty of the discrimination task). Perception tasks allow us to evaluate the impact of attention alone, as the duration of the retention period and the memory load are then very reduced.

By investigating in three experiments how distracting are non-relevant sounds presented during the encoding period, we could specify the link between attention and memory processes during encoding of non-verbal sounds. Given the nature of the task, performance was expected to depend highly on participants' musical expertise, hence in the princeps experiment, only non-musician participants are tested with the new MEMAT paradigm. In the second experiment, expertise effects on the various cognitive processes of interest were evaluated thanks to the testing of highly trained musician participants. Finally, the third experiment with non-musician listeners served to arbitrate between two alternative interpretations of the data.

EXPERIMENT 1: Memory and Attention manipulation in non-musicians

Non-musician participants were tested with a first version of the MEMAT protocol (MEMAT-1), where, as detailed below, the melodies to encode were always accompanied by a distracting melody.

Methods

Participants

Sixteen paid non-musician participants (all right-handed, 4 men and 12 women, aged 20-33 years) participated in the first experiment. Participants were considered as non-musicians when they never practiced any instrument nor singing outside compulsory educative programs.

All participants were free from neurological or psychiatric disorder and had normal hearing and normal or corrected-to-normal vision. All participants gave their written informed consent to participate. Experimental procedures were approved by the appropriate regional ethics committee.

Neuropsychological tests and questionnaires

Participants were asked to perform subtests of the WAIS (Working Memory subtest: digit span forwards, backwards, and ascending, arithmetic; Processing Speed subtest: codes, symbols). They also had to fill-in self-evaluation questionnaires about their attention (Adult Self-Report Scale, Schweitzer et al. 2001 - going from 0 to 30, high scores indicating attentional difficulties), and their anxiety and depression level (Hospital Anxiety and Depression Scale, Zigmond, Snaith, 1983). Demographic and neuropsychological data are summarized in Table 1.

Variable	Experiment 1 MEMAT-1 non- musicians		Experiment 2 MEMAT-1 musicians		Group comparison Experiment 1 vs 2		Experiment 3 MEMAT-2 non- musicians		Group comparison Experiment 1 vs 3	
	mean	std	mean	std	BF ₁₀	error %	mean	std	BF ₁₀	error %
Gender	men: 4 women:12		men: 4 women:12		0.5	-	men: 5 women:11		0.9	-
Laterality	69.7	32.8	77.6	19.1	0.3	0.2 e-3	64.4	40.6	0.6	0.5 e-3
Years of music education	0.0	0.0	15.7	4.1	<i>5.4e+7*</i>	1.5e-11	0.0	0.0	-	-
Years of school education	15.7	1.2	14.9	1.3	0.6	0.6 e-3	16.4	1.1	1.1	0.1 e-1
Age (years)	23.8	3.7	23.4	2.8	0.3	0.2 e-3	23.6	2.4	0.3	0.2 e-3
Attention (ASRS)	4.6	2.6	5.5	5.0	0.3	0.2 e-3	5.3	3.2	0.4	0.1 e-3
Anxiety (HAD-1)	9.4	4.2	7.2	3.6	0.8	0.9 e-3	6.9	4.2	0.9	0.9 e-3
Depression (HAD-2)	3.4	2.0	3.0	2.0	0.3	0.2 e-3	2.5	2.1	0.4	9.6 e-4
WM WAIS Index	103.9	3.1	112.6	12.5	1.1	0.1 e-1	106.1	10.9	0.3	8.8 e-4
WM: Sub-test Span Forward	10.8	1.4	11.6	2.2	0.4	8.3 e-4	10.7	2.3	0.3	0.1 e-3
WM: Sub-test Span backwards	8.7	1.3	10.8	2.3	<i>4.7</i>	2.6 e-5	8.9	1.9	0.3	0.2 e-3
WM: Sub-test Span ascendant	10.2	1.5	10.3	2.8	0.3	0.2 e-3	11.3	2.5	0.9	0.9 e-3
WM: Sub-test Arithmetic	15.4	3.5	16.6	2.4	0.3	0.2 e-3	15.8	3.0	0.3	0.2 e-3
Speed WAIS Index	112.0	13.7	121.9	16.8	0.5	0.2 e-3	113.8	9.3	0.3	0.2 e-3
Speed: Sub- test Codes	82.1	11.7	93.3	17.9	1.4	0.8 e-3	85.8	5.0	0.6	0.4 e-3
Speed: Sub- test Symbols	103.9	13.1	93.3	18.0	0.3	0.2 e-3	85.8	8.9	0.3	0.2 e-3

Table 1- Demographic and questionnaire information for all groups of participants. For each variable, mean and standard deviation (std) for each group are given, as well as the Bayesian Factors (BF₁₀) for the comparison between groups (contingency table for gender, t-test otherwise). Positive to decisive evidences against the null hypothesis are highlighted in bold and italics. Laterality: Edinburgh index, %; ASRS: Adult ADHD Self-Report Scale, from 0 to 18; HAD: Hospital Anxiety and Depression scale, HAD-1 from 0 to 21, HAD-2 from 0 to 21; each sub-test of the WAIS from 1 to 19; WAIS Indexes are composite notes derived from the raw scores ranging from 46 to 154, where 100 is the average performance in the population. *: One sample t-test for comparison to zero of musicians' data.

Material

96 four-note-long melodies were created using random combinations of eight-harmonic synthetic tones from the C major scale, spanning two octaves between 110 Hz and 440 Hz. The maximal interval between any two notes of a melody is 7 semi-tones. notes are 250-ms long and the interval between notes (offset to onset) is 250 milliseconds.

In each melody, there are no consecutive identical notes. Every melody contains at least an ascending and a descending interval. For the perception tasks, a fifth note is added at the end of the melody, that can be either identical or different from the previous one.

Attention manipulation

S1 (the melody to encode) and DIS (the distracting melody to filter out) are nested, but not played simultaneously. S1 is played in the indicated ear (see below), and DIS is played in the other ear, each note one after the other. The first sound to be played is the first note of S1, and the last note to be played is the last note of DIS.

The DIS melodies can be rather easy (easy DIS) or hard (hard DIS) to filter. An easy DIS melody is composed of notes in a frequency range separated by 5-tones from the corresponding S1 melody frequency range (higher or lower in pitch). A hard DIS melody frequency range is the same than the corresponding S1 melody frequency range. DIS melodies are constructed with the same rules as for the S1 melodies, as described above.

Memory task

During the memory task, for each trial (see Figure 23-A.), the participant is informed of the ear of interest by an arrow presented during 800 ms (all visual contents are seven-centimeter-wide black elements displayed individually at the center of a white screen located at ~75cm from the participants' eyes). After the presentation of this arrow, the melody of interest (S1) and the distracting melody (DIS) are played in the headphones, in the ear of interest and in the other ear, respectively. After a 2000-ms pause, during which a cross is displayed on the screen, the melody (S2) to compare to S1 is presented in the ear of interest. The participant has then 2000 ms to answer to the question "Is S2 identical or different from S1?". When S2 differs from S1, only one note out of four differs, and it can be either the second, third, or fourth one, never the first one which would be too salient. The answer period starts at the end of the S2 melody, and an answer terminates the trial. When the participant does not answer within 2000 ms, a message indicating that no answer was recorded is displayed on the screen before the next trial.

In the low memory load task (low-M), when S2 differs from S1, one note is replaced by another which is 6 semi-tones apart (ascending or descending) and induces a change in the melody contour. In the high memory load task (high-M), when S2 differs from S1, the changed note differs from the original one only by 1 or 2 semi-tones (always in the C-major scale) and does not induce a change in the melody contour.

Perception task

In the Perception task (see Figure 23-B.), the participant is informed of the ear of interest by an 800-ms-long arrow displayed on the screen. After the arrow presentation, S1 and DIS melodies are played in the ear of interest and in the other ear, respectively. The participant has then to answer to the question “Are the last two tones of the melody of interest identical or different?”. The answer period starts at the end of S2, and any answer terminates the trial. When the participant does not answer, a message indicating that no answer was recorded is displayed on the screen before the next trial.

In the low perception load task (low-P), when the two last S1 notes are different, they are 3 or 4 semi-tones apart (always in the C-major scale), ascending or descending. In the high perception load task (high-P), when the two last S1 notes are different, they differ by a quarter tone, ascending or descending.

Procedure

Participants are seated in a comfortable armchair in a sound-attenuated room, at 75cm distance from the screen (1280x1024 pixels, 17”). All stimuli are delivered using Presentation software (Neurobehavioral Systems, Albany, CA, USA). Sounds are delivered through a set of Sennheiser HD 280 pro headphones. First, participants have to fill in questionnaires and undergo an audiogram to confirm their self-reported absence of auditory deficit. Second, they perform short training blocks (8 trials) for all four block types (two tasks x two loads). Training melodies (S1, DIS, and S2) are specific to the training sessions. Third, they perform the four experimental blocks (48 trials each), in the same order as the training blocks.

Trials last a maximum of 5300ms during the perception blocks, and a maximum of 8800ms during the memory blocks, leading to four-minute-long perception blocks, and six-minute-long memory blocks.

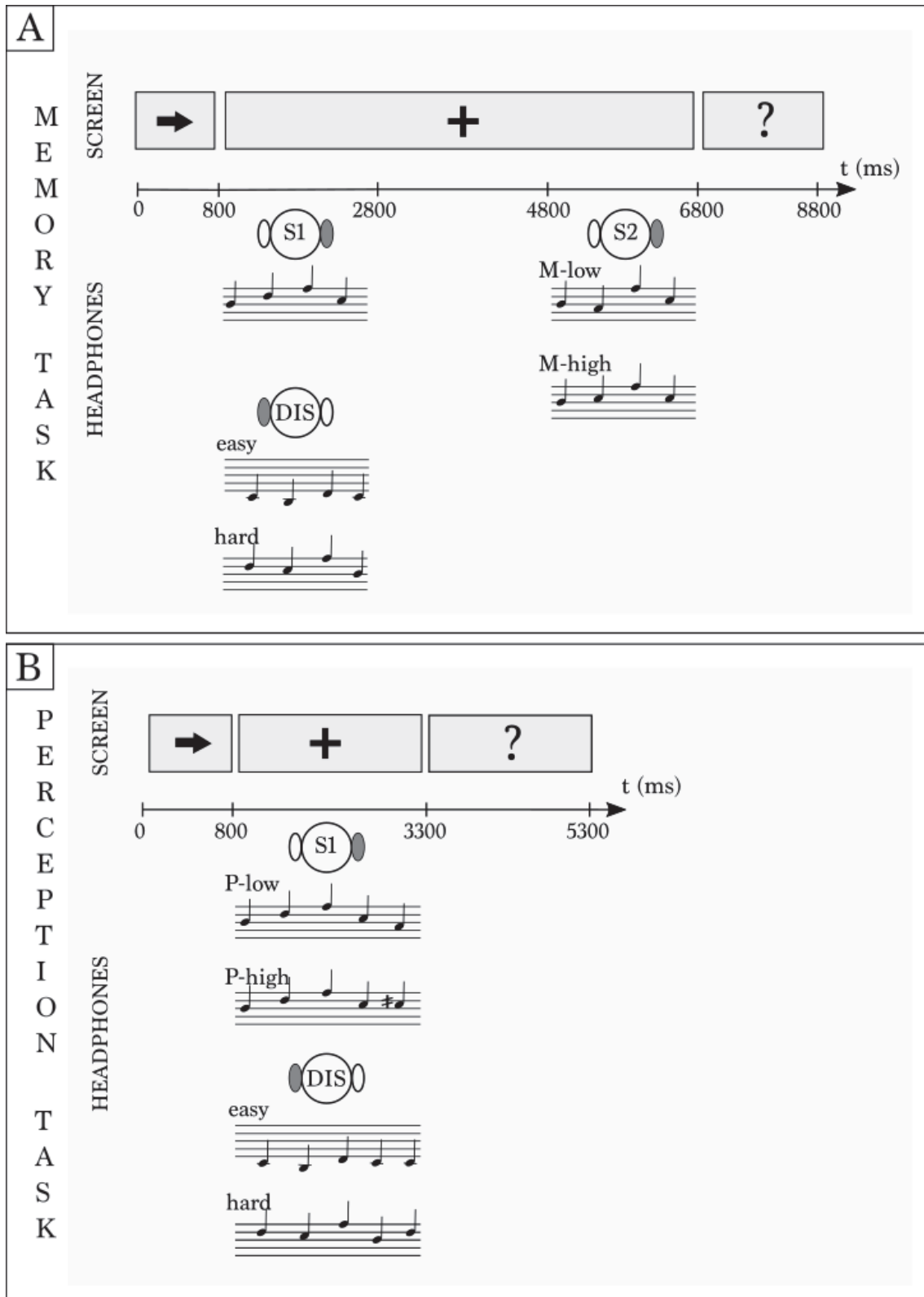


Figure 23 - Trial design in the Memory (A) and Perception (B) Tasks. Changed sounds are 6 semi-tones different from the original one in the low memory load task vs. 1 or 2 semitones in the high memory load task, and 3 or 4 semi-tones in the low perception load task, vs. a quarter tone in the high perception load task (the symbol \sharp represents here an ascending quarter tone).

Balancing – within blocks

Each block contains 48 trials. All the combinations of ear of interest (Left or Right), distractor difficulty (easy DIS or hard DIS), associated answer (same or different) are equiprobable within block (6 trials/block each). For each of these combinations with an expected answer “different”, the direction of the change is as likely to be ascendant or descendant in frequencies (3 trials/block each).

In the Perception task, the last two sounds of the DIS melody can be identical or different independently of the difference between the two last sounds of the S1 melody (equiprobable combinations within blocks).

This within-block balancing thus allows us to control for side, expected answer, change direction, and (for the Perception task only) DIS last tones effects.

Balancing – between blocks

For a given participant, the same S1 melodies are used in all blocks. However, for a given S1 melody, the answer, the direction of the change in S2 when different, the level of DIS difficulty, and the side of presentation are balanced across blocks.

Block orders are balanced between subjects (Latin square). For half of the participants, melodies S1 and DIS are inverted and become respectively DIS and S1.

Association between one S1 melody and another DIS melody changes across participants, enabling us to limit the impact in the results from any unfortunate easy or difficult match.

Data Analysis

Trial rejection

Trials in which participants gave no answer, several answers, or did answer at an inappropriate moment (i.e. outside of the indicated period) are excluded from analysis. The average number of valid trials is 185.4 (± 5.7 , standard deviation) out of 192 trials per participant. There is no evidence for any significant difference of the number of trials rejected between the different combinations of the main variables (task, task load, difficulty of the distracting melody; Bayesian repeated-measure ANOVA: $BF_{10} < 0.77$).

Measurements

Performance was assessed using signal detection theory indexes. d' is the difference between normalized “Hits” and normalized “False alarms”. Hits are the proportion of correct “different” answer over all “different” trials, and False alarms are the proportion of incorrect “different” answer over all “same” trials.

Criterion (c) indicates the response bias. Positive values indicate the tendency of answering “same” and negative values reflect the tendency of answering “different”.

Median Reaction Times (RTs) are computed out of correctly answered trials and correspond to the time between the end of the sound (*i.e.* S1+DIS in the perception blocks, and S2 in the memory blocks irrespective of the change position in S2) and the button press.

Main statistical analyses

d' and c were submitted to a Bayesian repeated-measure ANOVA with TASKload (difficulty of the task, two levels: low, high), DISdiff (difficulty of the DIStractor, two levels: easy DIS, hard DIS) and TASK (two levels: Memory [M], Perception [P]) as within-participant factors. Additionally, criterion for each main factor combination (TASKload x DISdiff x TASK) were submitted to a Bayesian one-sample t-test comparison to zero.

RTs (and d' for completeness) were submitted to a Bayesian repeated-measure ANOVA with TASKload (difficulty of the task, two levels: low, high), DISdiff (difficulty of the DIStractor, two levels: easy DIS, hard DIS), separately for Memory and Perception tasks. The different trial temporal structures in the two tasks (see Fig. 1) precluded a joint analysis of RTs.

Post-hoc comparisons for significant effects or interactions were conducted using Bayesian t-tests.

We reported Bayes Factor (BF_{10}) as a relative measure of evidence of a given model (compared to the null model). To interpret the strength of evidence against the null model, we considered a BF between 1 and 3 as weak evidence, a BF between 3 and 10 as positive evidence, a BF between 10 and 100 as strong evidence and a BF higher than 100 as a decisive evidence (Lee & Wagenmakers, 2014). Similarly, to interpret the strength of evidence in favor of the null model, we considered a BF between 0.33 and 1 as weak evidence, a BF between 0.01 and 0.33 as positive evidence, a BF between 0.001 and 0.01 as strong evidence and a BF lower than 0.001 as a decisive evidence.

Additionally, we report for each factor and interaction the BF inclusion that compares models that contain the effect to equivalent models stripped of the effect and was considered as a relative measure of evidence supporting the inclusion of a factor.

All statistical analyses were conducted using the software JASP (Wagenmakers et al., 2018).

Results – MEMAT 1, non-musician listeners

For d' (Figure 24A-1, Sup.Table 1Sup.Table 2), the best model explaining all Memory and Perception results of MEMAT-1 in non-musicians is the one with factors TASK, TASKload, DISdiff and the interaction between TASKload and DISdiff ($BF_{10}=1.3e+11$). There is decisive evidence for TASKload ($BF_{inclusion}=3.7e+6$) and for DISdiff ($BF_{inclusion}=6.9e+4$), strong evidence for the TASK effect ($BF_{inclusion}=10.3$) and positive evidence for the TASKload x DISdiff interaction ($BF_{inclusion}=4.4$). There is positive evidence for no effect of the TASK x DISdiff interaction ($BF_{inclusion}=0.2$). Overall, d' 's were higher in the Memory task compared to the Perception task. In both tasks, d' are higher for easy-to-ignore distractors (easy DIS) compared to hard-to-ignore distracting melodies (hard DIS), and higher under low load compared to high load. Difference between hard DIS and easy DIS is less important when load is high compared to low. For the Memory task results analyzed alone, similar results are found (Memory: best model comprises TASKload, DISdiff and their interaction, $BF_{10}=7.7e+7$; $BF_{inclusion}[TASKload]=479107.6$, $BF_{inclusion}[DISdiff]=1542.3$, $BF_{inclusion}[TASKload \times DISdiff]=3.1$; see Sup.Table 3Sup.Table 4). Post-hoc statistics indicate decisive evidence for a difference between DISdiff modalities under low memory load ($BF_{10}=665.6$) but weak evidence for any difference between DISdiff modalities under high memory load ($BF_{10}=1.3$). In the perception task alone, the interaction is not included in the best model (Perception: best model includes TASKload and DISdiff, $BF_{10}=395.0$; $BF_{inclusion}[TASKload]=24.4$, $BF_{inclusion}[DISdiff]=32.0$, $BF_{inclusion}[TASKload \times DISdiff]=1.0$; Sup.Table 5Sup.Table 6).

For the criterion, in agreement with previous studies using delayed-matching-to-sample tests, there is weak evidence for positive c values or an absence of difference from zero (see Sup.Table 7), underlining that participants tended to miss differences between melodies. The best model explaining results from MEMAT-1 in non-musicians includes TASK, TASKload, diffDIS, and TASKxTASKload interaction ($BF_{10}=4894.8$). There is positive evidence for TASK effect ($BF_{inclusion}=5.9$) and decisive evidence for TASKload effect ($BF_{inclusion}=1297.1$): criterion is higher for the Perception than for the Memory task and is higher under high load than under low load (see Sup.Table 8 Sup.Table 9).

For the RTs (Figure 24A-2.), the best model explaining results from MEMAT-1 in non-musicians is the one with TASKload and DISdiff for the Memory task alone ($BF_{10}=661.0$; see Sup.Table 10) and the one with DISdiff for the Perception task alone ($BF_{10}=41.0$; Sup.Table

12). There is strong to decisive evidence for DISdiff effect in both tasks (Memory: $BF_{inclusion}=283.9$; Perception: $BF_{inclusion}=41.6$), and positive evidence for TASKload in the Memory task ($BF_{inclusion}=4.0$) (see Sup.Table 11 and Sup.Table 13).

In both tasks, RTs are longer for hard DIS compared to easy DIS. In the memory task only, RTs are longer under high load.

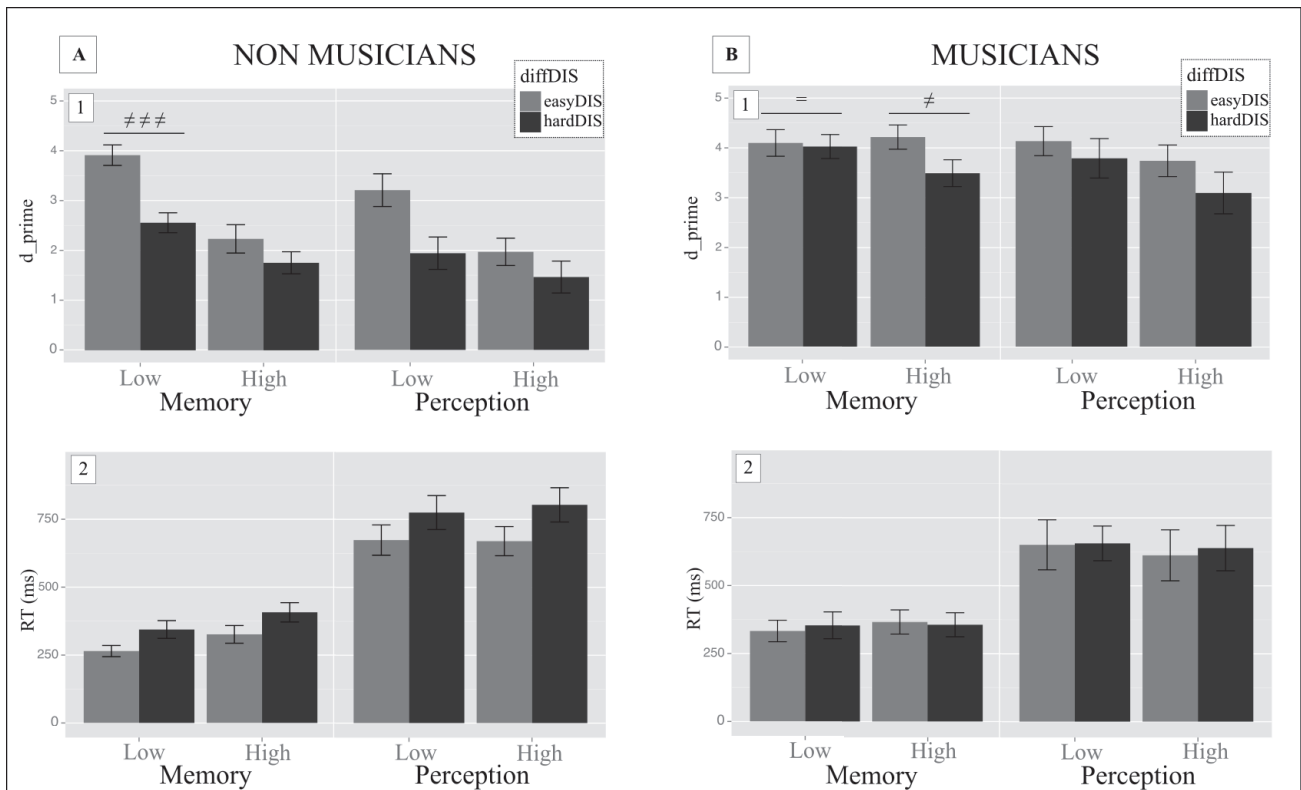


Figure 24 - Behavioral results of MEMAT-1, non-musician (A) and musician (B) participants. Effects of the distraction difficulty and task load on d' (1, top panels) and RT (2, bottom panels). Results of post-hoc t -tests of the TASKload by DISdiff interaction on d' in the Memory task: "###" corresponds to $BF > 100$ (decisive evidence), "≠" corresponds to $10 > BF > 3$ (positive evidence), "=" corresponds to $0.33 > BF > 0.1$ (positive evidence in favour of the null model)..

Discussion

Overall, the results of Experiment 1 confirm the expected influence of the difficulty levels for filtering the distractors and of the task loads. The hypothesized difficult distracting melodies indeed have a greater distracting impact than the easy ones, whatever the task is, in terms of both d' and RT (see Figure 24). High loads result in lower d' in both Perception and Memory tasks (and longer RTs in the Memory task), going along with a greater tendency to answer “same” (higher c), *i.e.* to miss differences. There is evidence for an absence of interaction between the distractor difficulty and the task on d' , meaning that the distractor impact is rather similar in both tasks. Criteria are higher for Perception than for Memory task, showing a greater tendency to answer “same” in the Perception Task. This might be due to a greater difficulty to spot a quarter tone and third intervals (Perception task) than second and fourth intervals (Memory task), explaining also the slight decrease of performance in the perception task. Nonetheless, performance in the Perception task confirm that participants can reliably perceive quarter tone and third intervals, which suggests that the memory performance will not be limited by perception difficulties.

In terms of d' , we observed evidence for an interaction between distractor difficulty and task load, especially in the memory task, which underlines greater distractor difficulty cost (hard minus easy DIS) for low compared to high memory load. This interaction effect points to shared resources between attention and memory processing. As a first step towards characterizing these shared resources and identifying possible separate resources, we decided to assess the effect of musical expertise on these processes (Experiment 2). It has indeed been established that musicians have enhanced WM capacities, especially for musical sounds (for a recent meta-analysis, see Talamini et al., 2016). Therefore, we expect musicians to be better at the memory task, in terms of d' and RT, and to be less impacted by the difficulty of the task. We also expect them to be better at the perception task, as their perception of musical tone differences has been reinforced by training. Does music expertise also impact attention performance? If yes, we would expect musicians to have lower distractor difficulty cost than non-musician. Conversely, an absence of an effect of musical expertise on attention performance would point towards some separate resources between memory and attention.

The interaction between distractor difficulty and task load observed in this first experiment can be explained in two different ways in light of the **cognitive** and **perceptual** load theories (Lavie et al., 2004; Lavie, 2005).

According to the **cognitive** load theory (Lavie et al., 2004; Lavie, 2005; Yi et al., 2004), under low load, there is enough spare cognitive resources to filter out easy-to-ignore distractors but not to suppress difficult-to-ignore distractors; while under higher load, the limited cognitive resources are devoted to the difficult memory task and less available to inhibit distractors, irrespective of their difficulty.

According to the **perceptual** load theory (Cartwright-Finch & Lavie, 2007; Forster & Lavie, 2007; Handy & Mangun, 2000; Huang-Pollock et al., 2002; Lavie, 1995; Lavie et al., 2014; Lavie & Cox, 1997; Lavie & Tsai, 1994), under low load, there is enough perceptual resources to process both relevant and irrelevant information, difficult-to-ignore distractors leading to greater interference; whereas under higher load, the limited perceptual resources are devoted to process relevant information and not available to process distractors, irrespective of their difficulty. Increasing difficulty/load would result in worse performance than under lower load, but similarly for easy and difficult-to-ignore distractors.

Therefore, both of these theories can explain this lower distractor difficulty cost for high than low memory load. However, these two theories lead to different predictions on performance in the absence of distracting melodies. Indeed, according to the **cognitive** load theory, in the high memory load task, there would be few resources available to inhibit even easy-to-filter-out distractors, resulting in strong interference and in worse performance than in the absence of distracting information. On the contrary, according to the **perceptual** load theory, in the high memory load task, there would be few resources available to process distractors, resulting in low interference and in similar performance in the presence or absence of distracting information.

To tip the scale towards one of the two models, we performed a third experiment using a new experimental condition: the absence of distracting melodies (MEMAT-2). As memory load is more likely to act as a cognitive load, we predict results in agreement with the cognitive load theory. However, as this MEMAT task also relies on encoding of a perceptive attribute, results in line with the perceptual load theory are not to exclude.

EXPERIMENT 2: Memory and Attention manipulation, impact of musical expertise

Musicians have greater WM capacities than non-musicians (Talamini et al., 2020; Talamini et al., 2017). To test if music expertise also impacts attentional capacities, we tested musicians with the same paradigm as in Experiment 1 (MEMAT-1).

Methods

Participants

Sixteen paid musician participants (all right-handed, 4 men and 12 women, aged 18-34 years) took part in the second experiment. They were professional musicians or conservatory students. They were matched to the non-musician participants included in Experiment 1 in terms of school education, age, laterality and gender (see Table 1).

All participants were free from neurological or psychiatric disorder and had normal hearing and normal or corrected-to-normal vision. All subjects gave their written informed consent to participate. Experimental procedures were approved by the appropriate regional ethics committee.

Psychological tests and questionnaires

Participants were asked to perform the same subtests of the WAIS and questionnaires as in Experiment 1 (digit span forward, backward, and ascending, arithmetic, codes, and symbols; ASRS, HAD).

Experiment

The experiment was MEMAT-1, the exact same one as described in Experiment 1.

Statistical Analysis

Bayesian t-tests were led between the two groups (musicians from Experiment 2 and non-musicians from Experiment 1) for all demographic information and questionnaire results, except for musical education. All non-musician participants had zero year of practice of music, leading to a null variance, so we tested musicians' musical expertise in comparison to zero thanks to a one-sample Bayesian t-test.

In the musician group, we first performed the same Bayesian analysis of d' and c with both tasks, as described in non-musicians in Experiment 1, and the same post-hoc analysis. Then,

we present the ANOVAs computed on each task separately for an easier step-by-step analysis and interpretation.

For each task separately, we also compared results (d' , RT) from Experiments 1 and 2, *i.e.* results of non-musicians and musicians under MEMAT-1 experiment, thanks to a Bayesian repeated-measure ANOVA with TASKload (difficulty of the task, two levels: low, high), DISdiff (difficulty of the DIStractor, two levels: easy DIS, hard DIS as within-participant factors, and GROUP (two levels: musicians, non-musicians) as a between-participant factor. Planned t-tests were performed between easy DIS and hard DIS conditions under each Task load (Low/High) in each group.

For each task separately, DIS difficulty cost (easy minus hard DIS) and load cost (low minus high load) were computed in terms of d' . To assess the effect of musical expertise on attentional filtering and task load, four planned Bayesian t-tests have been computed to compare groups for each cost (DIS difficulty cost, load cost) of each task (Memory, Perception).

Results

Group comparisons: Demographics and neuropsychological data

Bayesian t-tests confirm that the two groups were matched in school education, age, laterality and gender ($0.3 < BF_{10} < 0.6$; see Table 1). Also, as expected, there is decisive evidence ($BF_{10} = 5.4e+7$) for a significant musical education level different from zero for the musician participants.

Bayesian t-tests show weak evidence for no difference in Attention, Anxiety and Depression scores from ASRS and HAD questionnaires ($BF_{10} \leq 0.8$)

There is a positive evidence for better performance in musicians (10.8 +/- 2.3 std) compared to non-musicians (8.7 +/- 1.3 std) in the backwards digit span test ($BF_{10} = 4.7$), confirming better WM capacities in musicians.

There is weak evidence for better performance in musicians (93.3 +/- 17.9 std) compared to non-musicians (82.1 +/- 11.7 std) in the code test ($BF_{10} = 1.4$).

In the other subtests, there was weak to positive evidence for no difference between musicians and non-musicians ($0.3 < BF_{10} \leq 0.5$).

Musicians: Main results

For d' (Figure 24B-1., Sup.Table 14Sup.Table 15), the best model explaining all Memory and Perception results of MEMAT-1 in musicians is the one with factors TASKload and DISdiff ($BF_{10} = 54.3$). There is positive evidence for TASKload ($BF_{inclusion} = 4.7$) and strong evidence for DISdiff ($BF_{inclusion} = 15.8$) effects. Performance is better for easy-to-ignore distractors and for low load tasks.

For the Memory task alone (see Sup.Table 16Sup.Table 17), the best model is the same as in non-musicians (Memory: best model comprises TASKload, DISdiff, and their interaction: $BF_{10} = 3.3$), even though it is close to the model with only DISdiff ($BF_{10} = 3.0$). There is weak evidence for the interaction effect ($BF_{inclusion} = 2.0$), and in a different way than for non-musician participants: for musicians, there is positive evidence for a difference between DISdiff levels under higher memory load ($BF_{10} = 9.1$), and for no difference between DISdiff levels under low memory load ($BF_{10} = 0.3$). There is positive evidence for the effect of DISdiff ($BF_{inclusion} = 3.1$), performance being better for easy-to-ignore distractors. There is weak evidence for no effect of TASKload ($BF_{inclusion} = 0.5$).

In the perception task alone, as in non-musicians, the interaction is not included in the best model (Perception: best model includes TASKload and DISdiff, $BF_{10}=9.9$; $BF_{inclusion}[TASKload]=4.3$, $BF_{inclusion}[DISdiff]=2.8$, $BF_{inclusion}[TASKload \times DISdiff]=0.3$; see Sup.Table 18Sup.Table 19).

For the criterion, all values are not significantly different from zero (see Sup.Table 7). The best model explaining results from MEMAT-1 in musicians includes TASKload only ($BF_{10}=9.8$). There is strong evidence for TASKload effect ($BF_{inclusion}=10.4$); criterion is significantly higher under high memory load than under low memory load. There is positive evidence for no effect of the interaction between TASK and TASKload ($BF_{inclusion}=0.3$) and of the interaction between TASK and DISdiff ($BF_{inclusion}=0.3$) (see Sup.Table 20Sup.Table 21).

For the RTs (Figure 24B-2.) the best model explaining the data is the null model, for both Memory and Perception tasks (see Sup.Table 22 and Sup.Table 24). In both tasks (see Sup.Table 23 Sup.Table 25), there is weak to positive evidence for no effect of TASKload (Memory: $BF_{inclusion} = 0.4$; Perception: $BF_{inclusion} = 0.3$), and of DISdiff (Memory: $BF_{inclusion} = 0.3$; Perception: $BF_{inclusion} = 0.3$).

Group comparisons (Non-musicians from Experiment 1 and Musicians from Experiment 2)

For d' , in the Memory task alone (see Sup.Table 26 and Sup.Table 27), the best model explaining data from MEMAT-1 in non-musicians and musicians is composed of the following factors: group, TASKload, group \times TASKload interaction, DISdiff, group \times DISdiff interaction, TASKload \times DISdiff interaction, group \times TASKload \times DISdiff interaction ($BF_{10} = 1.7e+15$). There is decisive evidence for an effect of the group ($BF_{inclusion} = 4.1e+10$), TASKload ($BF_{inclusion} = 1687.6$) and DISdiff ($BF_{inclusion} = 658.7$), strong evidence for an effect of the interaction between group and TASKload ($BF_{inclusion}=36.9$), and positive evidence for an effect of the interaction between group, TASKload and DISdiff ($BF_{inclusion}=3.1$). As reported above, there is decisive evidence for an effect of distractor difficulty under low memory load in non-musicians ($BF_{10} = 665.6$), with no effect of distractor difficulty under high memory load ($BF_{10} = 1.3$), while there is weak evidence for this effect of distractor difficulty but under high memory load in musicians ($BF_{10} = 9.1$) and not under low memory load ($BF_{10} = 0.3$, see Figure 24, top panels).

For the Perception task alone (see Sup.Table 28 and Sup.Table 29), the best model explaining the data from MEMAT-1 in non-musicians and musicians is composed of the factors group, TASKload and DISdiff ($BF_{10}=9.4e+8$). There are strong to decisive evidence for effects of these three factors (group: $BF_{inclusion}=4.1e+7$, TASKload: $BF_{inclusion}=17.0$, DISdiff: $BF_{inclusion}=13.7$), musicians having better performance than non-musicians.

For RTs, there is no better model than the null model to explain the data, in both tasks (see Sup.Table 30 and Sup.Table 32). There is no evidence for any effect from the different factors (see Sup.Table 31 and Sup.Table 33).

Overall, musicians are more accurate in their answers, but not especially faster to respond than non-musicians, and the pattern of performance according to task load and distractor difficulty differ in the two groups. This Group \times TASKload \times DISdiff interaction is further explored in the analysis of the distractor difficulty and memory load costs reported in the following.

In the Memory task, in terms of distractor difficulty and memory load costs on d' (see Figure 25-A), there is weak evidence for a difference of distractor difficulty cost between groups ($BF_{10} = 1.2$) and decisive evidence for a difference of memory load cost between groups ($BF_{10} = 106.2$).

Overall, musicians have smaller distractor difficulty and memory load costs than non-musicians, but what they really seem to stand out for is a reduced memory load cost. Whereas in non-musicians (Experiment 1) memory load cost was larger than distractor difficulty cost, the reverse pattern was observed in musicians (Experiment 2).

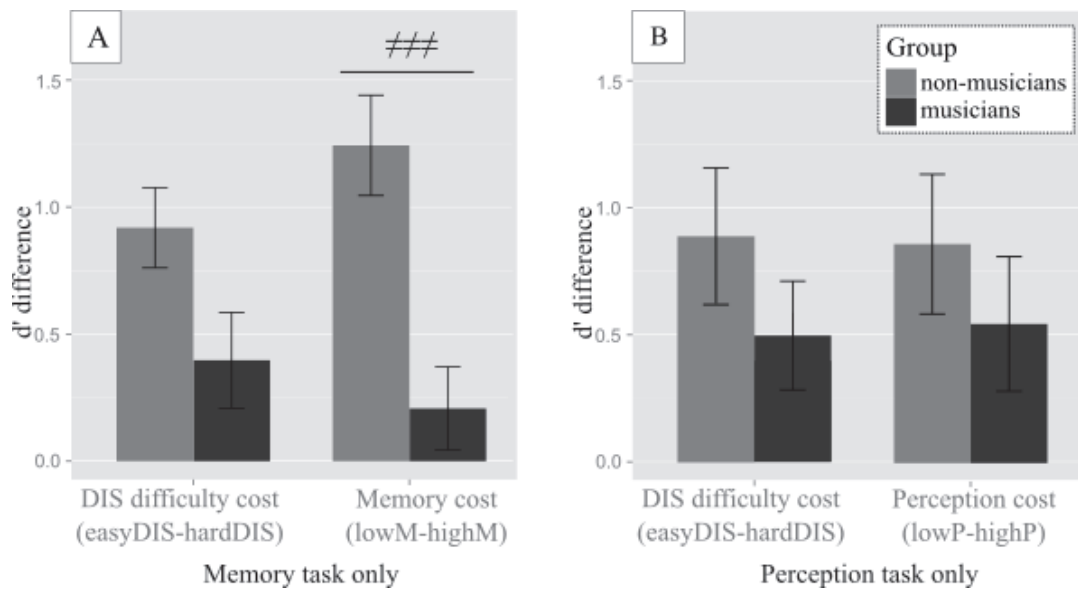


Figure 25 - Group comparison for distractor difficulty and memory (A) / perception (B) load costs on d' . Distractor difficulty cost is the difference between condition easy- and hard-to-ignore distractors under Memory (A) or Perception (B) tasks. Memory load cost is the difference between low and high memory load, Perception cost is the difference between low and high perception load. Results of planned t -tests between groups for each type of cost, in each task: ### = $BF > 100$ (decisive evidence against the null model),

In the Perception task, concerning distractor difficulty and perception load costs on d' (see Figure 25-B), there is weak evidence for no difference between groups for both costs ($BF=0.4$ in both cases).

Discussion

Musicians have overall better performance at the MEMAT task, with less errors for similar reaction times, in all conditions of task load or distractor difficulty. Comparing tones and melodies is an everyday training for musicians, which can explain that musician participants are overall more accurate than non-musicians in both Perception and Memory tasks. What is interesting here is that they do not all reach the maximum performance, showing that MEMAT is difficult enough to study WM and attention loads even on a population with expertise.

There is no difference of distractor difficulty cost in the Perception task between non-musicians and musicians, pointing towards an absence of difference between musicians and non-musicians in terms of attention filtering. On the contrary, increasing the memory load has a much weaker impact in musicians than in non-musicians, in agreement with studies showing better short-term memory capacities for tone sequences in musicians (Francesca Talamini et al., 2017). Differential impact of music expertise on Memory and Distractor difficulty costs is in favor of a dissociation, at least partial, between attention and WM processes.

The extent of musicians' WM advantage over the non-musician participants can also be addressed thanks to the results of the subtests of the WAIS, with only one (out of three measures) showing an advantage in musicians (backwards digit span). This points to some degree of dissociation between memory for verbal (numerical) material in the WAIS and memory for musical material in MEMAT (Albouy et al., 2019; Talamini et al., 2020). Overall this pattern of results is compatible with the results of the meta-analysis of working memory abilities in musically-trained participants of Talamini et al. (2017), which revealed a larger effect size for the improvement in tonal memory than for a possible improvement in verbal memory.

The enhanced tonal memory abilities in musicians help us to understand interactions between attention and memory. In musicians, the interaction between memory load and distractor difficulty on d' does not follow the same pattern as for non-musicians. In the low memory load condition, it seems that for musicians the difficulty of the overall task is very low, and the difficulty of distractors has no impact on performance. As the memory load becomes higher (high-M), hard-to ignore distractors induce a decrease in performance. An enhanced distractor interference with increasing load is incompatible with the perceptual load theory (Cartwright-Finch & Lavie, 2007; Forster & Lavie, 2007; Handy & Mangun, 2000; Huang-Pollock et al.,

2002; Lavie, 1995; Lavie et al., 2014; Lavie & Cox, 1997; Lavie & Tsal, 1994). Here, the observed scheme clearly goes in line with the cognitive load theory. When the task is really easy (low memory load in musicians), brain resources are not fully occupied by the memorization process and are available to suppress both easy and hard-to-ignore distractors. When the task gets harder (high memory load in musicians or low memory load in non-musicians), there are less resources available to filter out correctly hard-to-ignore distractors, but still enough to suppress easy-to-ignore distractors. When the task is really hard (high memory load in non-musicians), there are no spare resources to filter out distractors, irrespective of their difficulty. In the last experiment, we test more directly this account of MEMAT findings in terms of the cognitive load theory.

EXPERIMENT 3: MEMAT-2, arbitrate between cognitive or perceptual load

Can we explain the interaction between attention and WM during sound sequence encoding with the **cognitive** load theory or with the **perceptual** load theory? Experiment 2 already provides evidence in line with the cognitive load theory. In order to test more directly this question, we administered to non-musician participants an alternative version of MEMAT with only the Memory task, and a new condition with no distracting melody.

In the case of the **cognitive** load theory, we expect, in the high memory load task, better performance in the absence than in the presence of distracting information, since there would be few resources available to inhibit distractors.

On the contrary, in the case of the **perceptual** load theory, we predict, in the high memory load task, similar performance in the absence or presence of distracting information, since there would be few resources available to process distractors.

Methods

Participants

Sixteen paid non-musician participants (all right-handed, 5 men and 11 women, aged 19-28 years) participated in this third experiment. Participants were considered as non-musicians as they never practiced any instrument or singing outside compulsory educative programs. They were matched with previous non-musician participants (Experiment 1) in terms of school education, age, laterality and gender (see Table 1) so that results are comparable between Experiments 1 and 3.

All participants were free from neurological or psychiatric disorder and had normal hearing and normal or corrected-to-normal vision. All subjects gave their written informed consent to participate. Experimental procedures were approved by the appropriate regional ethics committee.

Neuropsychological tests and questionnaires

Participants were asked to perform the same subtests of the WAIS and questionnaires as in Experiments 1 and 2 (digit span forward, backward, and ascending, arithmetic, codes, and symbols; and ASRS, HAD).

Materials

Same materials as in experiments 1 and 2 were used in MEMAT-2. The same melodies were used for the new condition without distracting tones (no DIS).

Attention manipulation

As in MEMAT-1, S1 and DIS melodies are nested, but not played simultaneously. S1 is played in the indicated ear, and DIS is played in the other ear, each tone one after the other. The first sound to be played is the first sound of S1, and the last sound to be played is the last sound of DIS.

In MEMAT-2, the DIS melodies can be absent (no DIS), rather easy (easy DIS) or hard (hard DIS) to filter. Participants are informed of the difficulty of the distraction, which was not the case in MEMAT-1. When absent, S1 sounds are separated from one another by 250ms silent intervals, so that the rhythm of S1 does not change between no DIS, easy DIS, and hard DIS conditions. As in MEMAT-1, an easy DIS melody is composed of sounds in a frequency range separated by 5 tones from the corresponding S1 melody frequency range. A hard DIS melody frequency range is the same than the corresponding S1 melody frequency range. DIS melodies follow the same rules as S1 melodies, as described above.

Memory Task

In MEMAT-2, participants perform only one task, which is the Memory task described for MEMAT-1 above.

Procedure

As in Experiments 1 and 2, participants are seated in a comfortable armchair in a sound-attenuated room, at 75cm distance from the screen. All stimuli are delivered using Presentation software (Neurobehavioral Systems, Albany, CA, USA). Sounds are delivered through a set of headphones. First, participants have to fill in several questionnaires and undergo an audiogram. Second, they do the training for all block types (n=8 trials per training block). Training melodies (S1, DIS and S2) are specific to the training sessions. Third, they perform the experimental blocks (6x24 trials), in the same order as the training. The main difference from MEMAT-1 here is that they are informed not only of the difficulty of the task but also of the difficulty of the distractors. Trials last at most 8800ms, leading to ca. three-minute-long memory blocks.

Balancing – within blocks

All the combinations of ear of interest (Left or Right), associated answer (same or different), direction of the change (ascendant or descendant frequencies) are equiprobable within block (3 trials/block each).

Balancing – between blocks

Participants perform 6 blocks (48 trials each), in which the load of the task (low-M and high-M) and the difficulty of the distractor (no DIS, easy DIS, and hard DIS) are kept constant. They are informed of the level of task and distractor difficulty. Please note that in MEMAT-2 the distractor difficulty is balanced between blocks rather than within block (MEMAT-1), to avoid mixing trials with and without distracting melodies.

The same S1 melodies are used in all blocks. However, the answer, the direction of the change when different, the level of DIS and the side of presentation are balanced across blocks. Blocks order (Latin square) and melody set for S1 and DIS (for half of the participants, S1 and DIS melodies are switched) are balanced across subjects.

Statistical Analysis

Similar statistical analyses as in Experiment 1 were conducted on the new non-musician group data. For the Bayesian repeated measure ANOVAs, the factor DISdiff has an additional level, leading to three levels: no DIS, easy DIS, hard DIS, and the factor TASK does not exist anymore.

The main objective of MEMAT-2 was to compare the condition no DIS and easy DIS, under high memory load in particular. To this aim, we planned and performed a Bayesian paired sample t-test comparing these two conditions under high memory load.

We also performed a Bayesian ANOVAs to compare RT and d' in the Memory task between MEMAT-1 and MEMAT-2 with DISdiff as a within-group factor (difficulty of the distractors, two levels: easy DIS and hard DIS), and EXP (Experiment, two levels: 1 or 3) as a between-group factor. As in Experiments 1 and 2, post-hoc tests are Bayesian t-tests. Planned comparisons between easy DIS and hard DIS conditions were performed through Bayesian paired sample t-tests, allowing us to dig into similarities and differences between MEMAT-1 and MEMAT-2 results.

Results

Main Results

For d' (Figure 26-A, Sup.Table 34 and Sup.Table 35), the best model explaining all Memory results of MEMAT-2 in non-musicians is composed of the factors TASKload and DISdiff ($BF_{10} = 1.8e+11$), with decisive evidence for both TASKload ($BF_{inclusion} = 3.5e+6$) and DISdiff factors ($BF_{inclusion} = 1.6e+7$). Participants are more accurate in the low memory load than in the high memory load task. They are more accurate in the no DIS than in the easy DIS ($BF_{10} = 512.7$), in the easy DIS than in the hard DIS ($BF_{10} = 55.7$), and in the no DIS than in the hard DIS ($BF_{10}=40887.5$) conditions.

As planned, we also statistically compared d' in the no DIS and easy DIS conditions under high memory load, enabling us to conclude in favor of one of our two hypotheses. We found positive evidence for a difference between no DIS and easy DIS conditions under high memory load ($BF_{10} = 14.1$).

For the criterion, all values are superior or equal to zero (see Sup.Table 7). The best model explaining results from MEMAT-2 in non-musicians includes TASKload ($BF_{10}=135.3$). There is decisive evidence for TASKload effect ($BF_{inclusion}=140.7$): criterion is significantly higher under high memory load than under low memory load. There is positive evidence for no effect of DISdiff ($BF_{inclusion}=0.3$) and for no effect of the interaction between TASKload and DISdiff ($BF_{inclusion}=0.3$) (see Sup.Table 36 Sup.Table 37).

For RTs (Figure 26-B), the best model explaining results from MEMAT-2 in non-musicians is the one composed of the factor DISdiff ($BF_{10} = 40.0$, see Sup.Table 38). There is strong evidence for a DISdiff effect ($BF_{inclusion}=39.6$), and positive evidence for no effect of TASKload ($BF_{inclusion}=0.2$) (see Sup.Table 39). There is positive evidence for longer RTs in the hard DIS than in the no DIS ($BF_{10} = 5.7$) and easy DIS ($BF_{10} = 7.8$) conditions, and there is positive evidence for no difference between no DIS and easy DIS conditions ($BF_{10} = 0.2$).

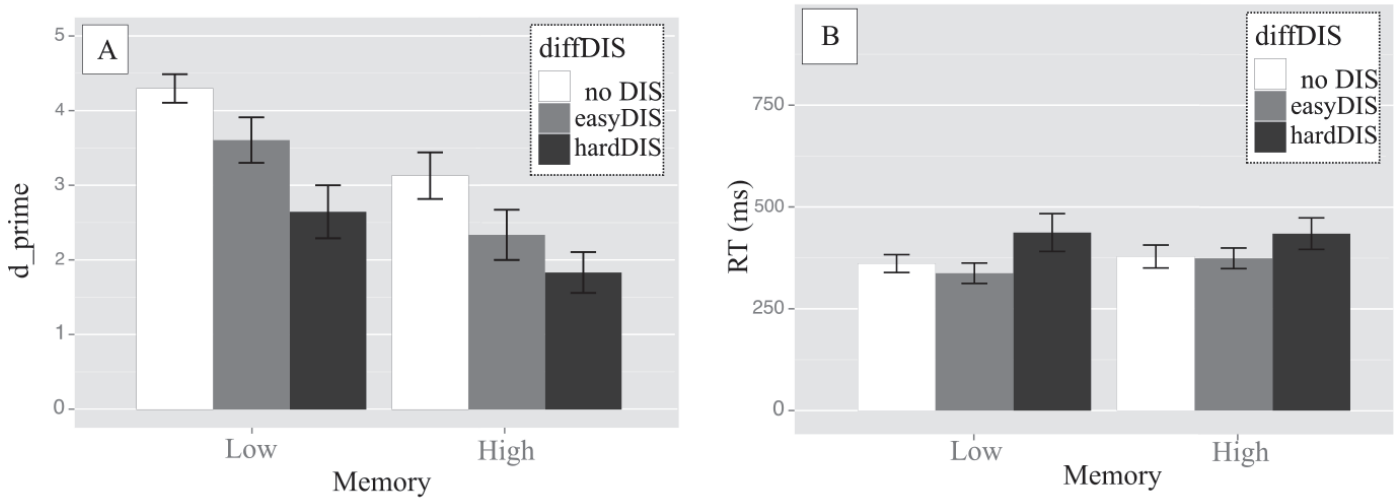


Figure 26 - Behavioral results of MEMAT-2, non-musician participants. Effects of the distraction and task levels on d -primes (A) and RTs (B).

Comparison between MEMAT-1 (in non-musicians) and MEMAT-2

For d' (see Sup.Table 40 and Sup.Table 41), the best model explaining both MEMAT-1 and MEMAT-2 results in non-musicians is composed of factors TASKload and DISdiff and their interaction ($BF_{10}=6.4e+9$). There is decisive evidence for both TASKload ($BF_{inclusion}=1.5e+7$) and DISdiff effect ($BF_{inclusion}=4442.8$), and weak evidence for an effect of their interaction ($BF_{inclusion}=1.3$). Also, there is positive evidence for no EXP effect ($BF_{inclusion}=0.2$), and no evidence for all interactions with the factor EXP ($BF_{inclusion} \leq 0.4$; see Sup.Table 41).

For RTs (see Sup.Table 42 Sup.Table 43), the best model explaining both MEMAT-1 and MEMAT-2 results on non-musicians is composed of factors EXP and DISdiff only ($BF_{10}=2139.2$). There is positive evidence for EXP effect ($BF_{inclusion}=9.3$), but all interactions with the factor EXP have no significant effect on the data ($BF_{inclusion} \leq 0.4$; see Sup.Table 43).

Discussion

We found better performance in the absence of distractors compared to the presence of easy-to-ignore distractors, including under high memory load. This result underlines a strong distractor interference under high memory load and the requirement of cognitive treatment to inhibit the easy-to-ignore distractors. Therefore, this finding does not fit with the perceptual load theory which predicts powerful irrelevant information filtering under high load, and clearly goes in line with the **cognitive** load theory (Lavie et al., 2004; Lavie, 2005; Yi et al., 2004).

Statistical analyses reveal no evidence for an impact of the experiment (MEMAT-1 vs. MEMAT-2) on the results. However, the interaction between DISdiff and TASKload present in MEMAT-1 was not observed when analyzing the results of MEMAT-2 alone. This can be explained by the change of information given to the participant. In MEMAT-1, participants were aware of the difficulty of the task only, whereas in MEMAT-2, there were aware of both task and distractors difficulties, preventing from surprise and confusion in the absence of the distracting melody, but enabling them to develop better strategies or put more effort to filter hard distractors in the dedicated block. There is no evidence towards a difference between experiments in terms of d' , and no change in the overall shape of the results, as there is still a greater difference between hard and easy DIS under low memory load than in the high memory load.

General Discussion

MEMAT paradigm allows us to study more closely attention, working memory (WM), and their interaction during encoding, in the auditory non-verbal domain. As accuracy is reduced with increasing difficulty of the distractor and of the task, both manipulations are validated. The isolated impact of distractors on perception can be measured in the Perception task, the impact of memory difficulty independently of any attentional filtering processes can be assessed in the Memory task in the absence of distractor, and the interaction between Attention and Memory can be evaluated in the Memory task in the presence of distractors.

In non-musicians, an impact of the task load on the size of the distractor difficulty cost in the memory task points at shared resources between attention and working memory processing. Better performance in the absence of distractors compared to the presence of easy-to-ignore distractors, especially under higher memory load, is in agreement with the cognitive load theory (i.e. shared cognitive resources between attention and memory). The pattern of results in musician participants, which show enhanced auditory memory skills confirmed that when the memory task is easier, more cognitive resources are available to efficiently filter out distracting melodies. However, musicianship is associated to considerably enhanced working memory performance in the auditory non-verbal domain but has less impact on distractor difficulty cost. This result pattern suggests some separate attention and working memory processes, in addition to the common cognitive resources highlighted above.

Shared resources between Attention and Memory: Perceptual Load Theory and Cognitive Load theory

Perceptual and Cognitive load theories allow to disentangle mechanisms internal to selective attention (Wenger & Fitousi, 2010). The Perceptual load theory proposes the automatic exclusion of irrelevant information in conditions of high perceptual load, i.e. when all perceptual resources are devoted to relevant information processing (Cartwright-Finch & Lavie, 2007; Forster & Lavie, 2007; Handy & Mangun, 2000; Huang-Pollock et al., 2002; Lavie, 1995; Lavie et al., 2014; Lavie & Cox, 1997; Lavie & Tsal, 1994); whereas the Cognitive load theory suggests the active inhibition of irrelevant information thanks to a cognitive mechanism requiring cognitive resources, only available under low cognitive load (Lavie et al., 2004; Lavie, 2005; Yi et al., 2004). These non-exclusive theories propose two different modes for filtering out distractors. Importantly, according to the Perceptual load theory,

increasing perceptual load results in reduced distractor interference; whereas according to the Cognitive load theory, increasing cognitive load leads to enhanced distractor interference.

In the present study, in non-musicians, under high memory load a lack of difference in performance between distracting sound filtering difficulties is observed, while better performances are found in the absence of distractor. This result suggests that the increased difficulty in the working memory process leads to less available cognitive resources for attention processes, i.e. filtering out of distracting sounds irrespective of their difficulty. Moreover, thanks to their better working memory capacities, musicians have no difficulty to filter all distractors in the low memory load task, but things get harder when the memory load is high. This can be explained by their ability to do the memory task using less cognitive resources than non-musicians, allowing them to easily filter distractors in the low memory load task. Their performance in the high memory load task are then similar to the performance of non-musicians in the low memory load condition. These findings show that increasing the memory load of the task reduces the inhibition of distractors, in line with the Cognitive load theory, and are in agreement with previous visual (Lee et al., 2007; Moray, 1967; Yi et al., 2004) and auditory (Schröger, 1996) studies. Importantly, this finding extends the Cognitive load theory to the encoding of non-verbal auditory material and suggests that the filtering out of distractors in the MEMAT task seems to be rather supported by an active inhibitory mechanism of irrelevant information.

Consequently, in MEMAT, the distractor difficulty cost can be considered as an indicator of the quantity of cognitive resources available for active attentional filtering mechanisms: when the difference between difficult distractors and easy distractors is important, it means that there are still some available resources for filtering, at least in the easy DIS condition. When this difference is reduced, it can be because in both conditions, there are no resources left (as in the high load condition for non-musicians), or because there are enough resources to inhibit all distractors (as in the low load condition, in musicians, see also below).

One reason that could explain why the present data are in line with the Cognitive Load Theory is that the MEMAT paradigm puts participant in an overall low perceptual load. Indeed, in studies revealing how perceptual load determines failure or success of selective attention, all relevant and irrelevant information were presented in the same stream in the high load condition, in studies mostly conducted in the visual modality (Johnson et al., 2002; Lavie, 1995; Wilson et al., 2008). In our case, pieces of information are indeed intricated but not overlapping, leading to demanding yet easier discrimination between relevant and irrelevant information.

Attention and Memory in musicians

In agreement with numerous previous studies, our results show that musicians have better performance than non-musicians in terms of working memory for musical stimuli (Ding et al., 2018; George & Coch, 2011; Kishon-Rabin et al., 2011; Tierney et al., 2008), in particular when the memory task is difficult. Results from the perception task also reveal better pitch discrimination performance for musicians compared to non-musicians, which is coherent with previous studies (Ding et al., 2018; George & Coch, 2011; Pallesen et al., 2010; Tierney et al., 2008). MEMAT allows us to add that these superior pitch discrimination and memory abilities are present even with irrelevant stimuli to filter.

Importantly, there was no major difference between musicians and non-musicians in terms of attention filtering. Previous research has however pointed out better selective attention in musicians, especially in the auditory domain (Baumann et al., 2008; Strait & Kraus, 2011), but it appears that these enhanced capacities are correlated with overall improvement in cognitive tasks (Strait et al., 2010), and are very likely to depend on working memory enhancement (Clayton et al., 2016). Improvement of working memory would “leave room” for better attentional processes (see also the previous paragraph). This allows us to underline that attention and working memory are at least partly distinct processes, with only superior working memory skills in musician participants, and attentional filtering skills within the normal range. We can thus tentatively speculate that musicianship is associated to better encoding strategies for musical material (e.g., within a tonal loop, as proposed by Schulze et al., 2011, involving in particular contour encoding processes, Talamini et al., 2020), but at a level of processing that is fairly independent from cognitive resources shared with attentional processes.

Specificities and usefulness of the MEMAT paradigm

Working Memory and Attention are very intricate processes. Only a few paradigms have tried disentangling them, and rarely so in the auditory domain. Especially, very few paradigms have been designed to manipulate both of them in an independent way. Delayed-Matching-to-Sample paradigms combined with selective speech-in-noise tasks might recruit specific language processing networks (Berouti et al., 1979; Rottschy et al., 2012), and paradigms combining auditory and visual modalities (Meck, 1984; Ward, 1982) might recruit several perceptual and integrative systems. With this new MEMory and ATtention (MEMAT) paradigm, we propose here a new way to manipulate attention and working memory using simple melodies.

Behavioral evidences for an interaction between attention filtering and working memory seem promising for further electrophysiological enquiries, for which MEMAT is particularly well designed. Indeed, each melody is used once for each condition (low or high difficulty of the task, easy or hard distractor, presentation to the left or right ear, presentation as a target or as a distractor) which allows all kinds of comparison between conditions. Both attention and WM involve frontal and temporal lobes (Albouy et al., 2013; Awh & Jonides, 2001; Bidet-Caulet et al., 2010) and impact on the amplitude of the N1 evoked response (Albouy et al., 2013; Awh & Jonides, 2001; Campbell et al., 2007). Further experiments are needed to explore the interaction between attention and memory during encoding in terms of cerebral correlates. It will be interesting to uncover the neural correlates for these two essential cognitive processes when they are manipulated during sound sequence encoding, allowing us on a longer term to specify how, when and where attention and working memory interact in the healthy brain and in populations of patients. If a brain mechanism is involved in both Attention and Working Memory, impact of both difficulty of the distractor and difficulty of the task should be similar on the related brain responses. Among other things, this paradigm can also help us to understand the impact of distraction during encoding on the cognitive effort during the retention period. Neurophysiological investigations using MEMAT should bring interesting insight into the shared and separate mechanisms of attention filtering and working memory.

Conclusion

To sum up, the MEMAT paradigm allows us to study the impact of memory load on attention filtering, and vice-versa, during sound sequence encoding, emphasizing the role of shared cognitive resources between memory and attention. The use of non-verbal auditory stimuli will allow for example further experiments along the course of development in children, without the confounding factor of verbal skills. The MEMAT paradigm has also been specifically designed to be used in neuroimaging experiments, thus allowing for an investigation of attention, working memory, and their interaction at the neurophysiological level.

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Supplementary data

MEMAT-1, non-musicians

d'

ANOVA on *d'* – non musicians, MEMAT-1, Memory and Perception tasks, with TASK, TASKload and DISdiff as factors

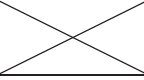
M & P	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 non-musicians	Null model (incl. subject)	0.053	3.4e-12	6.1e-11	1.0	X
	task	0.053	6.833e-12	1.2e-10	2.0	1.1
	TASKload	0.053	3.4e-7	6.1e-6	100965.7	2.3
	task + TASKload	0.053	1.3e-6	2.4e-5	388657.8	2.4
	task +TASKload+task * TASKload	0.053	5.1e-7	9.2e-6	151676.9	1.4
	DISdiff	0.053	7.2e-9	1.3e-7	2142.3	1.7
	task + DISdiff	0.053	2.3e-8	4.1e-7	6705.1	5.6
	TASKload + DISdiff	0.053	1.2e-2	0.2	3.6e+9	3.1
	task + TASKload + DISdiff	0.053	0.1	1.9	2.8e+10	2.2
	task + TASKload + DISdiff + task * TASKload	0.053	4.2e-2	0.8	1.2e+10	1.9
	task + DISdiff + task * DISdiff	0.053	5.7e-9	1.0e-7	1682.2	3.0
	task + TASKload + DISdiff + task * DISdiff	0.053	2.4e-2	0.4	7.1e+9	4.3
	task + TASKload + DISdiff + task * TASKload + task * DISdiff	0.053	1.1e-2	0.2	3.3e+9	1.6
	TASKload + DISdiff + TASKload * DISdiff	0.053	3.9e-2	0.7	1.2e+10	15.6
	task + TASKload + DISdiff + TASKload * DISdiff	0.053	0.4	13.6	1.3e+11	4.1
	task + TASKload + DISdiff + task * TASKload + TASKload * DISdiff	0.053	0.2	4.0	5.5e+10	3.7
	task + TASKload + DISdiff + task * DISdiff + TASKload *DISdiff	0.053	0.1	2.0	3.0e+10	9.8
	task + TASKload + DISdiff + task * TASKload +task*DISdiff + TASKload * DISdiff	0.053	4.9e-2	0.9	1.5e+10	4.5
	task + TASKload + DISdiff + task * TASKload +task*DISdiff + TASKload * DISdiff + task * TASKload * DISdiff	0.053	1.5e-2	0.3	4.4e+9	5.3

*Sup. Table 1 - Bayesian ANOVA results for *d'*, non-musicians, MEMAT-1 (factors: task, TASKload, DISdiff).*

M & P		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT 1 non-musicians	d'	task	0.263	0.5	10.3
		TASKload	0.263	0.1	3.7e +6
		DISdiff	0.263	0.1	6.9e+4
		task * TASKload	0.263	0.3	0.4
		task * DISdiff	0.263	0.2	0.2
		TASKload * DISdiff	0.263	0.8	4.4
		task * TASKload * DISdiff	0.053	1.5e-2	0.3

Sup.Table 2 - Analysis of effects for d', non-musicians, MEMAT-1, Perception and Memory Tasks (factors: task, TASKload, DISdiff).

ANOVA on d' - non musicians, MEMAT-1, Memory task, with TASKload and DISdiff as factors

MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 non-musicians	d'	Null model (incl. subject)	0.200	9.8e -9	3.9e -8	1.0	
		TASKload	0.200	1.6e -4	6.4e -4	16303.2	2.2
		DISdiff	0.200	5.0e -7	2.0e -6	51.5	0.9
		TASKload + DISdiff	0.200	0.2	1.3	2.5e +7	1.2
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.8	12.2	7.7e +7	1.5

Sup.Table 3 - Bayesian ANOVA results for d', non-musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 1 non-musicians	d'	TASKload	0.400	0.2	479107.6
		DISdiff	0.400	0.2	1542.3
		TASKload * DISdiff	0.200	0.8	3.1

Sup.Table 4 - Analysis of effects for results on d', non-musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

ANOVA on d' - non musicians, MEMAT-1, Perception task, with TASKload and DISdiff as factors

PERCEPTION		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 non-musicians	d'	Null model (incl. subject)	0.200	0.0	0.0	1.0	X
		TASKload	0.200	0.0	0.1	11.8	1.0
		DISdiff	0.200	0.0	0.1	15.7	0.8
		TASKload + DISdiff	0.200	0.5	3.9	395.0	1.3
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.5	3.6	379.5	10.4

Sup. Table 5 - Bayesian ANOVA results on d' for non-musicians, MEMAT-1, Perception Task only (factors: TASKload, DISdiff).

PERCEPTION		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT 1 non-musicians	d'	TASKload	0.400	0.5	24.4
		DISdiff	0.400	0.5	32.0
		TASKload * DISdiff	0.200	0.5	1.0

Sup. Table 6 - Analysis of effects for results on d' , non-musicians, MEMAT-1, Perception Task only (factors: TASKload, DISdiff).

Criterion

Criterion data: BF_{10} are extracted from comparison to zero (Bayesian one-sample t-test)

		Study 1 MEMAT 1, non-musicians			Study 2 MEMAT 1, musicians			Study 3 MEMAT 2, non-musicians		
		mean	SD	BF_{10}	mean	SD	BF_{10}	mean	SD	BF_{10}
Low Perception	Easy DIS	0.2	0.5	0.8	-5.9e-2	0.2	0.5			
	Hard DIS	0.1	0.4	0.4	1.0e-2	0.2	0.3			
High Perception	Easy DIS	0.6	0.6	25.4	0.3	0.5	2.4			
	Hard DIS	0.3	0.7	0.7	-8.6e-4	0.4	0.3			
Low Memory	No DIS							0.1	0.2	0.4
	Easy DIS	-0.1	0.4	0.5	-0.1	0.3	0.5	0.3	0.3	9.4
	Hard DIS	-0.2	0.5	1.6	-0.2	0.4	1.2	- 0.2e-2	0.6	0.3
High Memory	No DIS							0.4	0.5	6.5
	Easy DIS	0.4	0.4	27.9	4.7e-2	0.2	0.4	0.4	0.5	10.3
	Hard DIS	0.2	0.4	0.9	3.5e-2	0.4	0.3	0.4	0.4	22.0

Sup. Table 7 - Criterion data (mean, SD: standard deviation) on all experiments (MEMAT-1 non-musicians, MEMAT-1 musicians, MEMAT-2 non-musicians) and all crossed conditions (task, TASKload and DISdiff). BF_{10} are extracted from Bayesian one-sample test comparison to zero.

ANOVA on c - non musicians, MEMAT-1, Memory and Perception tasks, with task, TASKload and DISdiff as factors

M & P	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 non-musicians c	Null model (incl. subject)	0.053	3.1e -5	5.7e -4	1.0	
	task	0.053	1.1e -4	0.2e-2	3.6	6.9
	TASKload	0.053	2.3e-2	0.4	726.8	1.4
	task + TASKload	0.053	0.1	2.5	3921.7	5.9
	task + TASKload + task * TASKload	0.053	0.1	1.2	1953.0	1.6
	DISdiff	0.053	4.8e -5	8.6e -4	1.5	1.2
	task + DISdiff	0.053	1.7e -4	0.3e-2	5.4	1.4
	TASKload + DISdiff	0.053	4.7e-2	0.9	1505.1	2.7
	task + TASKload + DISdiff	0.053	0.3	7.1	8957.	3.9
	task + TASKload + DISdiff + task * TASKload	0.053	0.2	3.3	4894.8	2.6
	task + DISdiff + task * DISdiff	0.053	5.8e -5	0.1e-2	1.8	22.4
	task + TASKload + DISdiff + task * DISdiff	0.053	0.1	1.3	2155.1	2.2
	task + TASKload + DISdiff + task * TASKload + task * DISdiff	0.053	3.8e-2	0.7	1219.5	2.8
	TASKload + DISdiff +TASKload * DISdiff	0.053	1.5e-2	0.3	469.7	1.6
	task + TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	1.8	2936.6	4.3
	task + TASKload + DISdiff + task * TASKload + TASKload * DISdiff	0.053	0.1	1.0	1687.1	3.7
	task + TASKload + DISdiff + task * DISdiff + TASKload *DISdiff	0.053	2.4e-2	0.5	778.0	8.3
	task + TASKload + DISdiff + task * TASKload + task * DISdiff + TASKload * DISdiff	0.053	1.3e-2	0.2	407.4	3.5
task + TASKload + DISdiff + task * TASKload + task * DISdiff + TASKload * DISdiff + task * TASKload * DISdiff	0.053	0.4e-2	0.1	139.6	3.9	

Sup.Table 8 - Bayesian ANOVA results on criterion (c) for non-musicians, MEMAT-1, Memory and Perception Tasks (factors: task, TASKload, DISdiff).

M & P		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 1 non-musicians	c	task	0.263	0.5	5.9
		TASKload	0.263	0.5	1297.1
		DISdiff	0.263	0.5	2.3
		task * TASKload	0.263	0.3	0.5
		task * DISdiff	0.263	0.1	0.2
		TASKload * DISdiff	0.263	0.2	0.3
		task * TASKload * DISdiff	0.053	0.4e-2	0.3

Sup. Table 9 - Analysis of effects for results on criterion (c), non-musicians, MEMAT-1, Perception and Memory Tasks (factors: task, TASKload, DISdiff).

RT

ANOVA on RT - non musicians, MEMAT-1, Memory task, with TASKload and DISdiff as factors

MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 non-musicians	RT	Null model (incl. subject)	0.200	9.4e -4	0.4e-2	1.0	X
		TASKload	0.200	0.2e-2	0.7e-2	1.9	0.8
		DISdiff	0.200	0.2	0.7	164.8	1.4
		TASKload + DISdiff	0.200	0.6	6.5	661.0	2.0
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.2	1.1	236.0	5.7

Sup. Table 10 - Bayesian ANOVA results for results on RT, non-musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 1 non-musicians	RT	TASKload	0.400	0.6	4.0
		DISdiff	0.400	0.8	283.9
		TASKload * DISdiff	0.200	0.2	0.4

Sup. Table 11 - Analysis of effects for results on RT, non-musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

ANOVA on RT - non musicians, MEMAT-1, Perception task, with TASKload and DISdiff as factors

PERCEPTION		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 non-musicians	RT	Null model (incl. subject)	0.200	1.7e-2	0.1	1.0	X
		TASKload	0.200	0.4e-2	1.7e-2	0.3	1.0
		DISdiff	0.200	0.7	8.9	41.0	0.8
		TASKload + DISdiff	0.200	0.2	0.9	11.0	4.9
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.1	0.5	6.2	1.9

Sup. Table 12 - Bayesian ANOVA results for results on RT, non-musicians, MEMAT-1, Perception Task only (factors: TASKload, DISdiff).

PERCEPTION		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT 1 non-musicians	RT	TASKload	0.400	0.2	0.3
		DISdiff	0.400	0.9	41.6
		TASKload * DISdiff	0.200	0.1	0.6

Sup. Table 13 - Analysis of effects for results on RT, non-musicians, MEMAT-1, Perception Task only (factors: TASKload, DISdiff).

MEMAT-1, musicians

d'

ANOVA on d' - musicians, MEMAT-1, Memory and Perception tasks, with TASK, TASKload and DISdiff as factors

M & P	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 musicians	Null model (incl. subject)	0.053	0.4e-2	0.1	1.0	
	task	0.053	0.3e-2	4.7 e-2	0.7	0.9
	TASKload	0.053	1.3e-2	0.2	3.2	0.8
	task + TASKload	0.053	0.9 e-2	0.2	2.3	2.3
	task+TASKload+task*TASKloa	0.053	0.4 e-2	0.1	1.0	3.1
	DISdiff	0.053	4.3 e-2	0.8	11.0	0.9
	task + DISdiff	0.053	3.2 e-2	0.6	8.1	1.8
	TASKload + DISdiff	0.053	0.2	4.9	54.3	14.3
	task + TASKload + DISdiff	0.053	0.2	3.2	38.8	5.2
	task + TASKload + DISdiff + task * TASKload	0.053	0.1	1.4	17.9	7.5
	task + DISdiff +task * DISdiff	0.053	0.9 e-2	0.2	2.2	3.9
	task + TASKload + DISdiff + task * DISdiff	0.053	3.9 e-2	0.7	9.9	2.8
	task + TASKload + DISdiff + task * TASKload + task * DISdiff	0.053	1.7 e-2	0.3	4.2	2.2
	TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	3.1	37.1	1.9
	task + TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	2.7	33.0	6.1
	task + TASKload + DISdiff + task * TASKload + TASKload * DISdiff	0.053	0.1	1.1	14.5	3.3
	task + TASKload + DISdiff + task * DISdiff + TASKload *DISdiff	0.053	3.3 e-2	0.6	8.4	5.3
	task + TASKload + DISdiff + task * TASKload + task * DISdiff + TASKload * DISdiff	0.053	1.6 e-2	0.3	4.1	6.0
task + TASKload + DISdiff+ task*TASKload+task*DISdiff + TASKload * DISdiff + task * TASKload * DISdiff	0.053	0.7 e-2	0.1	1.7	4.3	

Sup.Table 14 - Bayesian ANOVA results for results on d', musicians, MEMAT-1 (factors: task, TASKload, DISdiff).

M & P		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 1 musicians	d'	task	0.263	0.3	0.8
		TASKload	0.263	0.4	4.7
		DISdiff	0.263	0.5	15.8
		task * TASKload	0.263	0.2	0.5
		task * DISdiff	0.263	0.1	0.3
		TASKload * DISdiff	0.263	0.4	0.8
		task * TASKload * DISdiff	0.053	0.7e-2	0.4

Sup.Table 15 - Analysis of effects for results on d', musicians, MEMAT-1, Perception and Memory Tasks (factors: task, TASKload, DISdiff).

ANOVA on d' - musicians, MEMAT-1, Memory task, with TASKload and DISdiff as factors

MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 musicians	d'	Null model (incl. subject)	0.200	0.1	0.5	1.0	X
		TASKload	0.200	0.1	0.2	0.5	1.4
		DISdiff	0.200	0.3	1.9	3.0	1.1
		TASKload + DISdiff	0.200	0.2	0.8	1.6	1.8
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.3	2.1	3.3	8.7

Sup.Table 16 - Bayesian ANOVA results on d', musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

MEMORY		Effects	P(inc)	P(incl da)	BF _{Inclusion}
MEMAT 1 musicians	d'	TASKload	0.400	0.2	0.5
		DISdiff	0.400	0.5	3.1
		TASKload * DISdiff	0.200	0.3	2.0

Sup.Table 17 - Analysis of effects for results on d', musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

ANOVA on d' - musicians, MEMAT-1, Perception task, with TASKload and DISdiff as factors

PERCEPTION		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 musicians	d'	Null model (incl. subject)	0.200	0.1	0.2	1.0	X
		TASKload	0.200	0.2	0.8	3.2	1.3
		DISdiff	0.200	0.1	0.5	2.0	1.5
		TASKload + DISdiff	0.200	0.5	4.1	9.9	10.6
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.2	0.8	3.4	2.1

Sup. Table 18 - Bayesian ANOVA results on d' , musicians, MEMAT-1, Perception Task only (factors: TASKload, DISdiff).

PERCEPTION		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT 1 musicians	d'	TASKload	0.400	0.7	4.3
		DISdiff	0.400	0.6	2.8
		<i>TASKload * DISdiff</i>	<i>0.200</i>	<i>0.2</i>	<i>0.3</i>

Sup. Table 19 - Analysis of effects for results on d' , musicians, MEMAT-1, Perception Task only (factors: TASKload, DISdiff).

Criterion

ANOVA on c - musicians, MEMAT-1, Memory and Perception tasks, with TASK, TASKload and DISdiff as factors

M & P	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 musicians c	Null model (incl. subject)	0.053	2.3e-2	0.4	1.0	X
	task	0.053	2.0e-2	0.4	0.9	1.9
	TASKload	0.053	0.2	5.2	9.8	1.5
	task + TASKload	0.053	0.2	4.6	8.9	1.2
	task+TASKload+task* TASKload	0.053	0.1	1.1	2.4	4.1
	DISdiff	0.053	1.1 e-2	0.2	0.5	0.8
	task + DISdiff	0.053	1.1 e-2	0.2	0.5	3.4
	TASKload + DISdiff	0.053	0.1	2.4	5.2	1.9
	task + TASKload + DISdiff	0.053	0.1	2.5	5.3	3.8
	task + TASKload + DISdiff + task * TASKload	0.053	3.2e-2	0.6	1.4	11.6
	task+DISdiff +task*DISdiff	0.053	0.3e-2	4.7e-2	0.1	2.0
	task + TASKload + DISdiff + task * DISdiff	0.053	3.1e-2	0.6	1.4	2.7
	task + TASKload + DISdiff +task* TASKload +task*DISdiff	0.053	0.8e-2	0.1	0.3	2.3
	TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	1.0	2.2	2.2
	task + TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	1.1	2.4	6.6
	task + TASKload + DISdiff + task * TASKload + TASKload * DISdiff	0.053	1.2e-2	0.2	0.6	4.6
	task + TASKload + DISdiff +task*DISdiff+ TASKload *DISdiff	0.053	1.4e-2	0.3	0.6	7.0
	task + TASKload + DISdiff +task* TASKload + task*DISdiff + TASKload * DISdiff	0.053	0.4e-2	0.1	0.2	12.4
task + TASKload + DISdiff + task * TASKload + task * DISdiff + TASKload * DISdiff + task * TASKload * DISdiff	0.053	0.5e-2	0.1	0.2	2.8	

Sup.Table 20 - Bayesian ANOVA results on criterion (c) for musicians, MEMAT-1, Memory and Perception Tasks (factors: task, TASKload, DISdiff).

M & P		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 1 musicians	c	task	0.263	0.4	1.0
		TASKload	0.263	0.7	10.4
		DISdiff	0.263	0.3	0.6
		<i>task * TASKload</i>	<i>0.263</i>	<i>0.1</i>	<i>0.3</i>
		<i>task * DISdiff</i>	<i>0.263</i>	<i>0.1</i>	<i>0.3</i>
		TASKload * DISdiff	0.263	0.1	0.4
		task * TASKload * DISdiff	0.053	0.5e-2	1.5

Sup. Table 21 - Analysis of effects for results on criterion (c), musicians, MEMAT-1, Memory and Perception Tasks (factors: task, TASKload, DISdiff).

RT

ANOVA on RT - musicians, MEMAT-1, Memory task, with TASKload and DISdiff as factors

MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 musicians	RT	Null model (incl. subject)	0.200	0.5	4.4	1.0	X
		TASKload	0.200	0.2	1.1	0.4	1.9
		DISdiff	0.200	0.2	0.7	0.3	0.9
		TASKload + DISdiff	0.200	0.1	0.3	0.1	5.4
		TASKload + DISdiff + TASKload * DISdiff	0.200	3.1e-2	0.1	0.1	3.3

Sup.Table 22 - Bayesian ANOVA results for results on RT, musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT 1 musicians	RT	TASKload	0.400	0.3	0.4
		<i>DISdiff</i>	<i>0.400</i>	<i>0.2</i>	<i>0.3</i>
		TASKload * DISdiff	0.200	3.1e-2	0.5

Sup.Table 23 - Analysis of effects for results on RT, musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

ANOVA on RT - musicians, MEMAT-1, Perception task, with TASKload and DISdiff factors

PERCEPTION		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 1 musicians	RT	Null model (incl. subject)	0.200	0.6	5.3	1.0	X
		TASKload	0.200	0.2	0.9	0.3	1.0
		DISdiff	0.200	0.2	0.8	0.3	1.4
		TASKload + DISdiff	0.200	0.1	0.2	0.1	1.7
		TASKload + DISdiff + TASKload * DISdiff	0.200	2.4e-2	0.1	4.2e-2	3.1

Sup.Table 24 - Bayesian ANOVA results for results on RT, musicians, MEMAT-1, Perception Task only (factors: TASKload, DISdiff).

PERCEPTION		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT 1 musicians	RT	<i>TASKload</i>	<i>0.400</i>	<i>0.2</i>	<i>0.3</i>
		<i>DISdiff</i>	<i>0.400</i>	<i>0.2</i>	<i>0.3</i>
		TASKload * DISdiff	0.200	2.4e-2	0.4

Sup.Table 25 - Analysis of effects for results on RT, musicians, MEMAT-1, Memory Task only (factors: TASKload, DISdiff).

MEMAT-1, comparison between non-musicians and musicians

d'

ANOVA on d' – non-musicians and musicians, MEMAT-1, Memory task only, with group, TASKload and DISdiff as factors

MEMORY	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT-1 non-musicians and musicians d'	Null model (incl. subject)	0.053	1.8e -16	3.2e -15	1.0	
	group	0.053	4.3e -8	7.8e -7	2.4e +8	2.9
	TASKload	0.053	8.0e -15	1.5e -13	45.0	5.1
	group + TASKload	0.053	2.4e -5	4.3e -4	1.3e +11	1.9
	group+TASKload +group*TASKload	0.053	4.1e -4	0.0	2.3e +12	1.7
	DISdiff	0.053	2.9e -15	5.2e -14	16.1	2.3
	group + DISdiff	0.053	5.2e -6	9.4e -5	2.9e +10	3.3
	TASKload + DISdiff	0.053	1.9e -13	3.5e -12	1074.9	1.9
	group + TASKload + DISdiff	0.053	0.8e-2	0.2	4.7e +13	2.7
	group + TASKload + group * TASKload + DISdiff	0.053	0.3	6.8	1.5e +15	3.6
	group + DISdiff + group * DISdiff	0.053	3.5e -6	6.3e -5	2.0e +10	2.3
	group + TASKload + DISdiff + group * DISdiff	0.053	0.006	0.1	3.6e +13	2.3
	group + TASKload + group * TASKload + DISdiff + group * DISdiff	0.053	0.2	5.4	1.3e +15	2.7
	TASKload + DISdiff + TASKload * DISdiff	0.053	5.1e -14	9.3e -13	288.2	3.8
	group + TASKload + DISdiff + TASKload * DISdiff	0.053	0.002	0.0	1.2e +13	2.6
	group + TASKload + group * TASKload + DISdiff + TASKload * DISdiff	0.053	0.08	1.6	4.5e +14	6.1
	group + TASKload + DISdiff + group*DISdiff+TASKload*DISdiff	0.053	0.002	0.0	9.6e +12	3.4
	group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	0.09	1.9	5.4e +14	31.7
	group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff + group * TASKload * DISdiff	0.5e-1	0.3	7.6	1.7e +15	3.0

Sup. Table 26 - Bayesian ANOVA results for results on d', non-musicians & musicians, MEMAT-1, Memory Task only (factors: group, TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT-1 non-musicians and musicians	d'	group	0.263	0.1e-1	4.1e +10
		TASKload	0.263	0.2e-1	1687.6
		DISdiff	0.263	0.3	658.7
		group * TASKload	0.263	0.7	36.9
		group * DISdiff	0.263	0.3	0.9
		<i>TASKload * DISdiff</i>	<i>0.263</i>	<i>0.2</i>	<i>0.3</i>
		group * TASKload * DISdiff	0.053	0.3	3.1

Sup. Table 27 - Analysis of effects for results on d', non-musicians & musicians, MEMAT-1, Memory Task only (factors: group, TASKload, DISdiff).

ANOVA on d' – non-musicians and musicians, MEMAT-1, Perception task only, with group, TASKload and DISdiff as factors

PERCEPTION	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT-1 non-musicians and musicians	Null model (incl. subject)	0.053	4.2e-10	7.5e-9	1.000	
	group	0.053	0.2e-2	0.04	5.3e+6	1.0
	TASKload	0.053	1.7e-9	3.1e-8	4.1	1.0
	group + TASKload	0.053	0.3e-1	0.5	6.8e+7	4.8
	group + TASKload + group * TASKload	0.053	0.9e-2	0.2	2.1e+7	4.4
	DISdiff	0.053	1.6e-9	2.9e-8	3.9	1.3
	group + DISdiff	0.053	0.2e-1	0.4	5.6e+7	1.0
	TASKload + DISdiff	0.053	7.8e-9	1.4e-7	18.7	2.5
	group + TASKload + DISdiff	0.053	0.4	11.6	9.4e+8	2.4
	group + TASKload + group * TASKload + DISdiff	0.053	0.1	2.6	3.0e+8	4.1
	group + DISdiff + group * DISdiff	0.053	0.8e-2	0.2	2.0e+7	3.5
	group + TASKload + DISdiff + group * DISdiff	0.053	0.2	3.4	3.8e+8	8.8
	group + TASKload + group * TASKload + DISdiff + group * DISdiff	0.053	0.4e-1	0.9	1.6e+8	4.3
	TASKload + DISdiff + TASKload * DISdiff	0.053	2.2e-9	4.0e-8	5.4	5.3
	group + TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	2.4	2.8e+8	5.7
	group + TASKload + group * TASKload + DISdiff + TASKload * DISdiff	0.053	0.4e-1	0.7	8.4e+7	2.7
	group + TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	0.4e-1	0.8	9.6e+7	4.0
	group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	0.1e-1	0.2	3.0e+7	5.3
group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	6.9e-4	0.01	0.3 e-3	5.8	

Sup. Table 28 - Bayesian ANOVA results for results on d' , non-musicians & musicians, MEMAT-1, Perception Task only (factors: group, TASKload, DISdiff).

PERCEPTION		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT-1 non-musicians and musicians	d'	group	0.263	0.6	4.1e +7
		TASKload	0.263	0.6	17.0
		DISdiff	0.263	0.5	13.7
		<i>group * TASKload</i>	<i>0.263</i>	<i>0.2</i>	<i>0.3</i>
		<i>group * DISdiff</i>	<i>0.263</i>	<i>0.3</i>	<i>0.4</i>
		<i>TASKload * DISdiff</i>	<i>0.263</i>	<i>0.2</i>	<i>0.3</i>
		<i>group * TASKload * DISdiff</i>	<i>0.053</i>	<i>0.007</i>	<i>0.5</i>

Sup.Table 29 - Analysis of effects for results on d', non-musicians & musicians, MEMAT-1, Perception Task only (factors: group, TASKload, DISdiff).

RT

ANOVA on RT – non-musicians and musicians, MEMAT-1, Memory task only, with group, TASKload and DISdiff as factors


MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT-1 non-musicians and musicians	RT	Null model (incl. subject)	0.053	0.2	5.7	1.0	X
		group	0.053	0.1	1.7	0.4	35.2
		TASKload	0.053	0.2	3.3	0.6	1.2
		group + TASKload	0.053	0.3 e-1	0.6	0.1	1.6
		group + TASKload + group * TASKload	0.053	0.1 e-1	0.2	0.1	3.6
		DISdiff	0.053	0.2	3.9	0.7	1.7
		group + DISdiff	0.053	0.4 e-1	0.8	0.2	1.9
		TASKload + DISdiff	0.053	0.1	2.4	0.5	1.9
		group + TASKload + DISdiff	0.053	0.2 e-1	0.5	0.1	2.1
		group + TASKload + group * TASKload + DISdiff	0.053	0.9 e-3	0.2	0.3 e-1	2.4
		group + DISdiff + group * DISdiff	0.053	0.2 e-2	0.5	0.1	3.2
		group + TASKload + DISdiff + group * DISdiff	0.053	0.2 e-1	0.3	0.1	2.1
		group + TASKload + group * TASKload + DISdiff + group * DISdiff	0.053	0.7 e-3	0.1	0.3 e-1	4.9
		TASKload + DISdiff + TASKload * DISdiff	0.053	0.3 e-1	0.5	0.1	2.1
		group + TASKload + DISdiff + TASKload * DISdiff	0.053	0.7 e-3	0.1	0.2 e-1	2.1
		group + TASKload + group * TASKload + DISdiff + TASKload * DISdiff	0.053	0.3 e-3	0.05	0.1	8.1
		group + TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	0.5 e-3	0.1	0.2 e-1	5.9
		group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	0.2 e-3	0.037	0.8 e-3	7.1
		group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff + group * TASKload * DISdiff	0.5e-1	6.9e-4	0.01	0.3 e-3	5.8

Sup. Table 30 - Bayesian ANOVA results for results on RT, non-musicians & musicians, MEMAT-1, Memory Task only (factors: group, TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT-1 non-musicians and musicians	RT	<i>group</i>	0.263	0.2	0.3
		TASKload	0.263	0.4	0.6
		DISdiff	0.263	0.4	0.7
		group * TASKload	0.263	0.03	0.4
		group * DISdiff	0.263	0.06	0.7
		<i>TASKload * DISdiff</i>	0.263	0.05	0.3
		<i>group * TASKload * DISdiff</i>	0.053	6.9e-4	0.3

Sup. Table 31 - Analysis of effects for results on RT, non-musicians & musicians, MEMAT-1, Memory Task only (factors: group, TASKload, DISdiff).

ANOVA on RT – non-musicians and musicians, MEMAT-1, Perception task only, with group, TASKload and DISdiff as factors

PERCEPTION		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT-1 non-musicians and musicians	RT	Null model (incl. subject)	0.053	0.2	4.8	1.0	
		group	0.053	0.23	7.0	1.3	1.8
		TASKload	0.053	0.04	0.8	0.2	1.3
		group + TASKload	0.053	0.06	1.0	0.3	5.2
		group + TASKload + group * TASKload	0.053	0.02	0.3	0.1	2.4
		DISdiff	0.053	0.1	2.1	0.5	1.5
		group + DISdiff	0.053	0.1	3.0	0.7	3.0
		TASKload + DISdiff	0.053	0.02	0.4	0.1	1.9
		group + TASKload + DISdiff	0.053	0.03	0.5	0.1	4.5
		group + TASKload + group * TASKload + DISdiff	0.053	0.008	0.1	0.03	4.9
		group + DISdiff + group * DISdiff	0.053	0.07	1.3	0.3	3.3
		group + TASKload + DISdiff + group * DISdiff	0.053	0.01	0.2	0.1	3.3
		group + TASKload + group * TASKload + DISdiff + group * DISdiff	0.053	0.003	0.1	0.01	2.9
		TASKload + DISdiff + TASKload * DISdiff	0.053	0.005	0.1	0.02	2.7
		group + TASKload + DISdiff + TASKload * DISdiff	0.053	0.007	0.1	0.03	2.6
		group + TASKload + group * TASKload + DISdiff + TASKload * DISdiff	0.053	0.002	0.03	0.009	3.8
		group + TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	0.003	0.1	0.01	3.8
		group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff	0.053	7.9e -4	0.01	0.04	3.3
		group + TASKload + group * TASKload + DISdiff + group * DISdiff + TASKload * DISdiff + group * TASKload * DISdiff	0.5e-1	3.3e -4	0.006	0.002	23.3

Sup. Table 32 - Bayesian ANOVA results for results on RT, non-musicians & musicians, MEMAT-1, Perception Task only (factors: group, TASKload, DISdiff).

PERCEPTION		Effects	P(ir)	P(incl da)	BF _{Incl}
MEMAT-1 non-musicians and musicians		group	0.20	0.5	1.3
		<i>TASKload</i>	0.20	0.2	0.2
		DISdiff	0.20	0.3	0.5
		<i>group * TASKload</i>	0.20	0.02	0.3
		<i>group * DISdiff</i>	0.20	0.08	0.4
		<i>TASKload * DISdiff</i>	0.20	0.02	0.3
		<i>group * TASKload * DISdiff</i>	0.00	3.3e -4	0.4

Sup. Table 33 - Analysis of effects for results on RT, non-musicians & musicians, MEMAT-1, Perception Task only (factors: group, TASKload, DISdiff).

MEMAT-2, non-musicians

d'

ANOVA on d' - non musicians, MEMAT-2, Memory task, with TASKload and DISdiff as factors (3 levels of DISdiff: noDIS, easyDIS, hardDIS)

MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 2 non-musicians	d'	Null model (incl. subject)	0.200	4.5e -12	1.8e -11	1.0	X
		TASKload	0.200	4.9e -8	1.9e -7	10743.2	0.7
		DISdiff	0.200	2.2e -7	9.0e -7	50107.6	8.5
		TASKload + DISdiff	0.200	0.8	15.0	1.8e +11	1.3
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.2	1.1	4.7e +10	2.4

Sup.Table 34 - Bayesian ANOVA results on d', non-musicians, MEMAT-2, Memory Task only (factors: TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 2 non-musicians	d'	TASKload	0.400	0.8	3.5e +6
		DISdiff	0.400	0.8	1.6e +7
		<i>TASKload * DISdiff</i>	<i>0.200</i>	<i>0.2</i>	<i>0.3</i>

Sup.Table 35 - Analysis of effects for results on d', non-musicians, MEMAT-2, Memory Task only (factors: TASKload, DISdiff).

Criterion

ANOVA on c – non-musicians, MEMAT-2, Memory task, with task, TASKload and DISdiff as factors (3 levels of DISdiff: noDIS, easyDIS, hardDIS)

MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 2 non-musicians	c	Null model (incl. subject)	0.200	0.5e-2	2.1e-2	1.0	X
		TASKload	0.200	0.7	10.0	135.3	1.3
		DISdiff	0.200	0.1e-2	0.5e-2	0.2	0.6
		TASKload + DISdiff	0.200	0.2	1.1	39.7	3.5
		TASKload + DISdiff + TASKload * DISdiff	0.200	0.1	0.3	13.3	1.7

Sup.Table 36 - Bayesian ANOVA results on c', non-musicians, MEMAT-2, Memory Task only (factors: TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 2 non-musicians	c	TASKload	0.400	0.9	140.7
		<i>DISdiff</i>	<i>0.400</i>	<i>0.2</i>	<i>0.3</i>
		<i>TASKload * DISdiff</i>	<i>0.200</i>	<i>0.1</i>	<i>0.3</i>

Sup.Table 37 - Analysis of effects for results on c, non-musicians, MEMAT-2, Memory Task only (factors: TASKload, DISdiff).

RT

ANOVA on RT – non-musicians, MEMAT-2, Memory task, with task, TASKload and DISdiff as factors (3 levels of DISdiff: noDIS, easyDIS, hardDIS)

MEMORY		Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT 2 non-musicians	RT	Null model (incl. subject)	0.200	1.9e-2	0.1	1.0	X
		TASKload	0.200	0.4e-2	1.7e-2	0.2	1.7
		DISdiff	0.200	0.8	13.7	40.0	1.7
		TASKload + DISdiff	0.200	0.2	0.8	8.4	1.6
		TASKload + DISdiff + TASKload * DISdiff	0.200	4.1e-2	0.2	2.1	2.4

Sup.Table 38 - Bayesian ANOVA results on RT, non-musicians, MEMAT-2, Memory Task only (factors: TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF _{Inclusion}
MEMAT 2 non-musicians	RT	<i>TASKload</i>	0.400	0.2	0.2
		DISdiff	0.400	0.9	39.6
		<i>TASKload * DISdiff</i>	0.200	4.1e-2	0.3

Sup.Table 39 - Analysis of effects for results on RT, non-musicians, MEMAT-2, Memory Task only (factors: TASKload, DISdiff).

Comparison between MEMAT-1 and MEMAT-2, non-musicians

d'

ANOVA on d' – non-musicians, MEMAT-1 and MEMAT-2, Memory task only, with EXP (experiment), TASKload and DISdiff as factors

MEMOR Y	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT-1 & MEMAT-2 non-musicians	Null model (incl. subject)	0.053	6.6e-11	1.2e-9	1.0	
	EXP	0.053	1.3e-11	2.3e-10	0.2	2.9
	TASKload	0.053	7.5e-5	0.1e-2	1.1e+6	3.1
	EXP + TASKload	0.053	1.4e-5	2.4e-4	204544.4	2.2
	EXP + TASKload + EXP * TASKload	0.053	3.8e-6	6.9e-5	57848.0	3.1
	DISdiff	0.053	2.2e-8	4.0e-7	332.2	0.9
	EXP + DISdiff	0.053	4.3e-9	7.7e-8	64.0	2.5
	TASKload + DISdiff	0.053	0.3	9.0	5.0e+9	4.5
	EXP + TASKload + DISdiff	0.053	0.1	1.1	8.8e+8	2.1
	EXP + TASKload + EXP * TASKload + DISdiff	0.053	1.9e-1	0.4	2.9e+8	5.7
	EXP + DISdiff + EXP * DISdiff	0.053	1.2e-9	2.1e-8	17.7	2.8
	EXP + TASKload + DISdiff + EXP * DISdiff	0.053	2.1e-2	0.4	3.2e+8	15.2
	EXP + TASKload + EXP * TASKload + DISdiff + EXP * DISdiff	0.053	0.5e-2	0.1	7.5e+7	2.4
	TASKload + DISdiff + TASKload * DISdiff	0.053	0.4	13.4	6.4e+9	2.4
	EXP + TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	1.6	1.2e+9	2.8
	EXP + TASKload + EXP * TASKload + DISdiff + TASKload * DISdiff	0.053	2.3e-2	0.4	3.5e+8	3.0
	EXP + TASKload + DISdiff + EXP * DISdiff + TASKload * DISdiff	0.053	2.3e-2	0.4	3.4e+8	2.9
	EXP + TASKload + EXP * TASKload + DISdiff + EXP * DISdiff + TASKload * DISdiff	0.053	0.7e-2	0.1	10.0e+7	5.3
EXP + TASKload + EXP * TASKload + DISdiff + EXP * DISdiff + TASKload * DISdiff + EXP * TASKload * DISdiff	0.053	0.3e-2	4.7e-2	3.9e+7	5.7	

Sup. Table 40 - Bayesian ANOVA results for results on d', non-musicians, MEMAT-1 & MEMAT-2, Memory Task only (factors: EXP, TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT-1 & MEMAT-2 non-musicians	d'	<i>EXP</i>	0.263	0.1	0.2
		TASKload	0.263	0.4	1.5e +7
		DISdiff	0.263	0.4	4442.8
		<i>EXP * TASKload</i>	0.263	0.1	0.3
		<i>EXP * DISdiff</i>	0.263	0.1	0.3
		TASKload * DISdiff	0.263	0.6	1.3
		EXP * TASKload * DISdiff	0.053	0.3e-2	0.4

Sup. Table 41 - Analysis of effects for results on d', non-musicians, MEMAT-1 & MEMAT-2, Memory Task only (factors: EXP, TASKload, DISdiff).

RT

ANOVA on RT – non-musicians, MEMAT-1 and MEMAT-2, Memory task only, with EXP (experiment), TASKload and DISdiff as factors

MEMORY	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
MEMAT-1 & MEMAT-2 non-musicians	Null model (incl. subject)	0.053	1.4e -4	0.3e-2	1.0	X
	EXP	0.053	8.0e -4	1.4e-2	5.6	0.9
	TASKload	0.053	8.5e -5	0.2e-2	0.6	1.1
	EXP + TASKload	0.053	5.3e -4	1.0e-2	3.7	4.8
	EXP +TASKload +EXP*TASKload	0.053	2.0e -4	0.4e-2	1.4	2.8
	DISdiff	0.053	3.4e-2	0.6	238.2	1.8
	EXP + DISdiff	0.053	0.3	7.9	2139.2	3.0
	TASKload + DISdiff	0.053	2.4e-2	0.4	164.8	2.4
	EXP + TASKload + DISdiff	0.053	0.2	5.3	1598.1	2.2
	EXP + TASKload + EXP * TASKload + DISdiff	0.053	0.1	1.9	654.6	3.2
	EXP + DISdiff + EXP * DISdiff	0.053	0.1	1.9	659.5	9.2
	EXP + TASKload + DISdiff + EXP * DISdiff	0.053	0.1	1.4	500.9	2.9
	EXP + TASKload+ EXP * DISdiff + EXP * TASKload + DISdiff	0.053	2.6e-2	0.5	182.2	3.4
	TASKload + DISdiff + TASKload * DISdiff	0.053	0.6e-2	0.1	43.3	3.1
	EXP + TASKload + DISdiff + TASKload * DISdiff	0.053	0.1	1.2	422.4	6.4
	EXP + TASKload + EXP * TASKload + DISdiff + TASKload * DISdiff	0.053	2.7e-2	0.5	190.9	3.5
	EXP + TASKload + DISdiff + EXP * DISdiff + TASKload * DISdiff	0.053	1.7e-2	0.3	115.5	3.6
	EXP + TASKload + EXP * TASKload + DISdiff + EXP * DISdiff + TASKload * DISdiff	0.053	0.7e-2	0.1	51.3	4.5
EXP + TASKload + EXP * TASKload + DISdiff +EXP*DISdiff +TASKload*DISdiff + EXP * TASKload * DISdiff	0.053	0.3e-2	4.8e-2	18.4	4.6	

Sup. Table 42 - Bayesian ANOVA results for results on RT, non-musicians, MEMAT-1 & MEMAT-2, Memory Task only (factors: EXP, TASKload, DISdiff).

MEMORY		Effects	P(incl)	P(incl data)	BF Inclusion
MEMAT-1 & MEMAT-2 non-musicians	RT	EXP	0.263	0.6	9.3
		TASKload	0.263	0.3	0.7
		DISdiff	0.263	0.7	389.5
		EXP * TASKload	0.263	0.2	0.4
		<i>EXP * DISdiff</i>	<i>0.263</i>	<i>0.2</i>	<i>0.3</i>
		<i>TASKload * DISdiff</i>	<i>0.263</i>	<i>0.1</i>	<i>0.3</i>
		EXP * TASKload * DISdiff	0.053	0.3e-2	0.4

Sup.Table 43 - Analysis of effects for results on RT, non-musicians, MEMAT-1 & MEMAT-2, Memory Task only (factors: EXP, TASKload, DISdiff).

**WORKING MEMORY AND SELECTIVE ATTENTION
IN LOW VERSUS HIGH FREQUENCY DREAM RECALLERS**

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These behavioral results correspond to the analysis of behavioral data collected during MEG recordings. They are presented as the first draft of a future article.

Abstract

MEMAT is a paradigm allowing to study the interplay between selective attention and working memory during memory encoding of non-verbal auditory stimuli. Participants have to listen to a melody in one ear, while ignoring a distracting melody in the other ear. After a delay, the melody they focused on has to be compared to a new melody. The difference to catch between these melodies can be easy or hard to spot, implying low or high memory load. The distractors can be easy or hard to ignore. In previous experiments, this paradigm allowed to show that working memory and selective attention share common cognitive resources, leading to a saturation of performance when both tasks become difficult. We also showed that being advantaged for working memory processes impact the interaction between attention and memory, with memory using less resources and thus leading more room for selective attention to be performed efficiently.

Here, we tested two groups of 11 participants with two different attentional profiles: low and high frequency dream recallers. These participants show effective differences in attentional performances, with better performances and lower reaction times for low compared to high frequency dream recallers. Furthermore, there is more resistance from low dream recallers to hard-to-ignore distractors.

These results will later allow to assess auditory attention and memory processes differences between low and high frequency dream recallers, using brain imaging measures.

Keywords

Dream frequency; Working Memory; Auditory; Non-verbal; Memory encoding; Selective Attention

Introduction

Our ability to carry out our daily actions is based on skillful and precise interactions between cognitive processes. Surrounded by an overwhelming amount of information, we are able to select only a part of it to focus on. Currently looking at this article, immersed in this page, the cognitive processes necessary for its understanding are turned towards the written words, their meaning, rather than the color of the table you may be sitting on, or other internal mental ideas (a future appointment, your potential fatigue, etc.). There is a selection of information, by facilitating relevant elements and inhibiting irrelevant elements: this process is called attention. Attention has been studied in many different ways: from resistance to salient disturbing elements to passive reaction to irregular streams of sounds and endogenous control of the information to focus on, it revealed the involvement of various processes. Here, we will focus on selective attention. Selective attention has been studied thanks to dichotic listening paradigms, in which participants had to focus on one stream of information, played in one ear, while ignoring another stream of sounds, played in the other ear (Hillyard et al., 1973).

With relevant items selected in your environment, there are several ways to use the information. In order to understand one sentence here, for example, you have to be able to read, so decode the visual input you have selected, understand the language, and when this is done correctly, each word is stored in working memory, so that an overall mental picture of the meaning of the sentence can be reconstructed. Here, we aim to focus on this last working memory process. Working memory is the ability to maintain and manipulate information during a limited period of time. The working memory process consists of three main steps: encoding, retention, and recall. Encoding is the time during which the information is available and is integrated thanks to the construction of memory traces. During the retention period, with the information not available anymore, memory traces are constantly updated in order to be maintained. During the recall period, there is an access to the memory traces in order to retrieve them. The manipulation of the information can occur during retention or retrieval, depending on the task.

Attention and working memory (WM) have been studied mostly separately, but more and more research projects in modern psychology and neuroscience try to decipher their impact on each other, to uncover their common resources and to characterize their cooperation (Awh & Jonides, 2001; Colflesh & Conway, 2007; Rutman et al., 2009).

Attention have been shown to impact each working memory step. Cued information have more chances than non-cued information to be **encoded** in working memory (Botta et al., 2010; Griffin & Nobre, 2003; Murray et al., 2011; Palmer, 1990; Schmidt et al., 2002). In change-detection tasks, the capacity to detect changes is drastically reduced in case of a lack of attention occurring during encoding (Mack & Rock, 1998; Rensink, 2002; Simons et al., 2000; Vogel et al., 1998).

During **retention**, the performance of attention demanding tasks disrupts the working memory process (Brown, 1958; Peterson & Peterson, 1959; Salthouse, 1975; Watkins et al., 1973), whether it is verbal or spatial (Phillips & Christie, 1977; Watkins et al., 1973). Shifts of spatial attention induced by controlled saccades also negatively impact working memory performances (Awh et al., 1998; Pearson & Sahraie, 2003; Postle et al., 2006; Smyth & Scholey, 1994). However, this effect is reduced for easier working memory tasks: attention is not necessary to single feature maintenance but is necessary for feature-conjunction maintenance and for information manipulation (Delvenne & Bruyer, 2004; Wheeler & Treisman, 2002). Such observations led to the attention-based rehearsal hypothesis (Awh et al., 2006; Rensink, 2000, 2002): attention seems to be necessary for rehearsal during the maintenance period.

Finally, presentation of task irrelevant probes during **retrieval** leads to poorer working memory performances in terms of reaction times and accuracy (Awh et al., 1998; Banbury et al., 2001; Jha, 2002). Increasing the number of distractors proved to reduce recall performance when intervening tasks are performed at retrieval (Lewandowsky et al., 2008).

The other way around, working memory can also guide attention. When searching for an item in a visual array while retaining another item in memory, there is a significant increase of the search time compared to no retention (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006). When the encoded item appears in the search array, it can even facilitate visual search: it is unlikely to be selected for an eye movement, and if the eyes lay upon it, fixation duration is shorter than for other items (Houtkamp & Roelfsema, 2006). The majority of studies about the encoding period report no difference of attentional guidance abilities for different loads to encode (for a review, see Olivers, 2008). One explanation could be that when the targets to look for change for each trial, the resources engaged in memory encoding of the item might not be available for attentional guidance, whatever the memory load is (Soto et al., 2008; Woodman et al., 2007).

Very few studies focused on auditory non-verbal selective attention and working memory interaction during encoding. In a previous study, we built a new paradigm allowing to investigate this interaction. This paradigm, called MEMAT, for MEMory and ATtention, allows to manipulate both selective attention and working memory in an independent way. Using melodies, MEMAT allows to reduce interference from language-specific processes. We showed that for high working memory load, the difference between easy and hard-to-ignore distracting sounds is smaller than under low memory load. This effect reflects a saturation of the involved cognitive resources: a difficult working memory task recruits more resources, leading to poorer distractors inhibition, whether they are easy or hard to ignore.

We have started to investigate inter-individual differences in the interaction between memory and attention. Several studies report enhanced working memory capacities in musicians compared to non-musicians (Talamini et al., 2020; Talamini et al., 2017). Therefore, musicians can be a category of population useful to test the interaction of working memory and selective attention, allowing to investigate how increased memory abilities impact on this interaction. Thanks to MEMAT, we confirmed these enhanced working memory abilities in musicians compared to non-musicians. Furthermore, in musicians, the interaction between memory load and distractor difficulty does not follow the same pattern as for non-musicians. In the low memory load condition, it seems that for musicians the difficulty of the overall task is very low, and the difficulty of distractors has no impact on performance. As the memory load becomes higher (high-M), hard-to ignore distractors induce a decrease in performance. When the task is really easy (low memory load in musicians), brain resources are not fully occupied by the memorization process and are available to suppress both easy and hard-to-ignore distractors. When the task gets harder (high memory load in musicians or low memory load in non-musicians), there are less resources available to filter out correctly hard-to-ignore distractors, but still enough to suppress easy-to-ignore distractors. When the task is really hard (high memory load in non-musicians), there are no spare resources to filter out distractors, irrespective of their difficulty.

These results in musicians led to the idea to investigate a mirror group, in which participants would have different profiles of attentional abilities, in order to see its effect on working memory and selective attention interaction. The first idea would be to compare groups with or without attentional disorder. However, MEMAT is a highly demanding task, which is quite hard. Therefore, we looked for categories of population with different attentional profiles but still able to perform the task without too much effort.

It is well known that several parameters impact attentional profile. Older participants are known to have more attentional difficulties than young adults. However, age also impacts working memory abilities, which would bias the investigation. Another parameter is correlated with attention performances: personality traits. We looked for categories in which personality traits could be different, with potential elements going in favor of various attentional profiles, and this led us to compare performance in the MEMAT paradigm between low and high frequency dream-recallers.

Low-frequency dream recallers (LDR) report dreams less than twice a month, whereas high-frequency dream recallers (LHR) can produce dream reports upon awakening at least 5 days a week. Extraversion and openness to experience has been shown to be correlated with higher frequency of dream reports (Hartmann et al., 1998; Schredl et al., 1997). Lesions in the temporo-parietal junction (TPJ) stops dream recall (Escera et al., 2003; Garcia-Garcia et al., 2008), and the TPJ belongs to the ventral attention orienting network (Corbetta et al., 2008; Shulman et al., 2010). Furthermore, there is an increase of spontaneous activity in the TPJ in HDR compared to LDR, all this leading to the hypothesis according to which HDR are more sensitive than LDR to the external world that surrounds them (Escera et al., 2003; Garcia-Garcia et al., 2008).

In parallel, the P3a, which can be interpreted as a marker of the attention orientation (Polich, 2007) has been shown to be greater in HDR compared to LDR, during wakefulness and during sleep (Eichenlaub et al., 2014). Finally, a study from 2013 showed that the decrease of alpha is more sustained in HDR than LDR in attentional tasks, showing a longer release of inhibition in HDR compared to LDR (Ruby et al., 2013).

As there is no report of working memory differences between LDR and HDR, this bundle of results led us to test and compare them for the MEMAT task.

Methods

Participants

Twenty-two paid non-musician participants (20 right-handed, 10 men and 12 women, aged 20-33 years) participated in the experiment. Participants were considered as non-musicians when they practiced less than 1 year of instrument or singing outside compulsory educative programs. Among them, 11 were low dream recallers (LDR, less than 2 dream recalled per month at awakening) and 11 high dream recallers (HDR, more than 5 dream recalls per week at awakening). Demographics are presented in Table 1.

All participants were free from neurological or psychiatric disorder and had normal hearing and normal vision. All subjects gave their written informed consent to participate. Experimental procedures were approved by the appropriate national ethics committee.

Neuropsychological tests and questionnaires

Participants were asked to perform a creativity test in which they had to invent possible alternative use for a chair, a teacup or a pen in a free monologous way during 2 minutes for each object (Guilford Alternative Use Task, GAUT) (Bonk, 1967).

They also had to fill in the State Trait Inventory Anxiety questionnaire about their anxiety state (STAI; Spielberger, 1983), the Big Five Inventory questionnaire for personality traits (BFI; John et al., 1991), and the Pittsburg questionnaire for sleep quality (PQSI; Buysse et al., 1988). Neuropsychological data are summarized in Table 2.

Variable	LDR		HDR		Group comparison LDR vs HDR		Whole group	
	mean	std	mean	std	BF ₁₀	error %	mean	std
Gender	men: 6 women: 5		men: 5 women: 6		0.5	 	men: 11 women: 11	
Laterality	left-handed: 1 right-handed: 10		left-handed: 1 right-handed: 10		0.7	 	left-handed: 2 right-handed: 20	
Years of music education	0.4	0.5	0.1	0.3	0.8	4e-3	0.1	0.4
Years of school education	15.9	1.9	15.2	2.2	0.5	6e-3	15.5	2.0
Age	23.5	3.6	24.0	3.0	0.4	5e-3	23.8	3.3
Hours of sleep	7.5	1.1	8.0	0.7	0.6	9e-3	7.7	0.9
Dream recall frequency (per week)	0.12	0.2	5.8	0.9	1.8e+11	1.9e-15	2.9	3.0
STAI: now	31.9	10.3	34.2	9.8	0.4	5e-3	33.0	9.8
STAI: usually	35.7	9.9	42.3	10.3	0.9	4e-3	39.0	10.4
BFI: opening	3.7	0.6	3.8	0.8	0.4	5e-3	3.7	0.7
BFI: control	3.8	0.7	3.4	0.7	0.6	8e-3	3.6	0.7
BFI: extraversion	3.4	0.8	3.2	0.7	0.5	5e-3	3.3	0.7
BFI: altruism	4.0	0.6	3.7	0.5	0.8	6e-3	3.9	0.6
BFI: nervousity	2.2	0.8	2.9	0.7	1.7	1e-3	2.5	0.8
PQSI	6.0	3.1	5.7	3.5	0.4	5e-3	5.9	3.2
GAUT	24.6	12.7	28.1	11.1	0.4	5e-3	26.4	11.8

Table 2 - Demographic and questionnaire information for all groups of participants. Mean and standard deviation (std) in each group, Bayesian Factors (BF₁₀) for the comparisons between groups (contingency table for gender and laterality, t-test otherwise). LDR: Low Dream Recaller, HDR: High Dream Recaller. STAI: State Trait Inventory Anxiety; BFI: Big Five Inventory; PQSI: Pittsburg Quality Sleep Index; GAUT: Guilford Alternative Use Test;

Stimuli

240 four-sounds-long melodies were created thanks to combinations of eight-harmonic synthetic sounds from the C major scale, spanning four octaves between 65 and 1046Hz. The maximal interval between any two sounds of a melody is 7 semi-tones. Sounds are 250-ms long and the interval between sounds (offset to onset) is 250 milliseconds.

In each melody, there is no consecutive identical sounds. Every melody contains at least an ascending and a descending interval.

Paradigm

Attention manipulation

The melody of interest (S1) and the distracting melody (DIS) melodies are nested, but not played simultaneously. S1 is played in the indicated ear (see below), and DIS is played in the other ear, each tone one after the other. The first sound to be played is the first tone of S1, and the last tone to be played is the last tone of DIS.

The DIS melodies can be rather easy (easy DIS) or hard (hard DIS) to filter. An easy DIS melody is composed of sounds in a frequency range 5-tone-higher (or lower) than the corresponding S1 melody frequency range. A hard DIS melody frequency range is the same than the corresponding S1 melody frequency range. DIS melodies are constructed with the same rules as for the S1 melodies, as described above.

Memory task

For each trial (see Figure 27), the participant is informed of the ear of interest by an arrow (all visual contents are seven-centimeter-wide black elements displayed individually at the center of a white screen). 800ms after the arrow presentation onset, S1 and DIS are played in the ear of interest and in the other ear, respectively. After a 2000-ms pause, during which a cross is displayed on the screen, the melody (S2) to compare to S1 is played in the ear of interest. The participant has then 2000 ms to answer to the question “Is S2 identical or different from S1?”. When S2 differs from S1, only one sound out of four differs, and it can be either the second, third, or fourth one, never the first one which would be too salient. The answer period starts at the end of the S2 melody.

In the low memory load task (low-M), when S2 differs from S1, one sound is replaced by another which is 4 tones apart (ascending or descending) and induces a change in the melody contour. In the high memory load task (high-M), when S2 differs from S1, the changed sound differs from the original one only by 1 tone and does not induce a change in the melody contour.

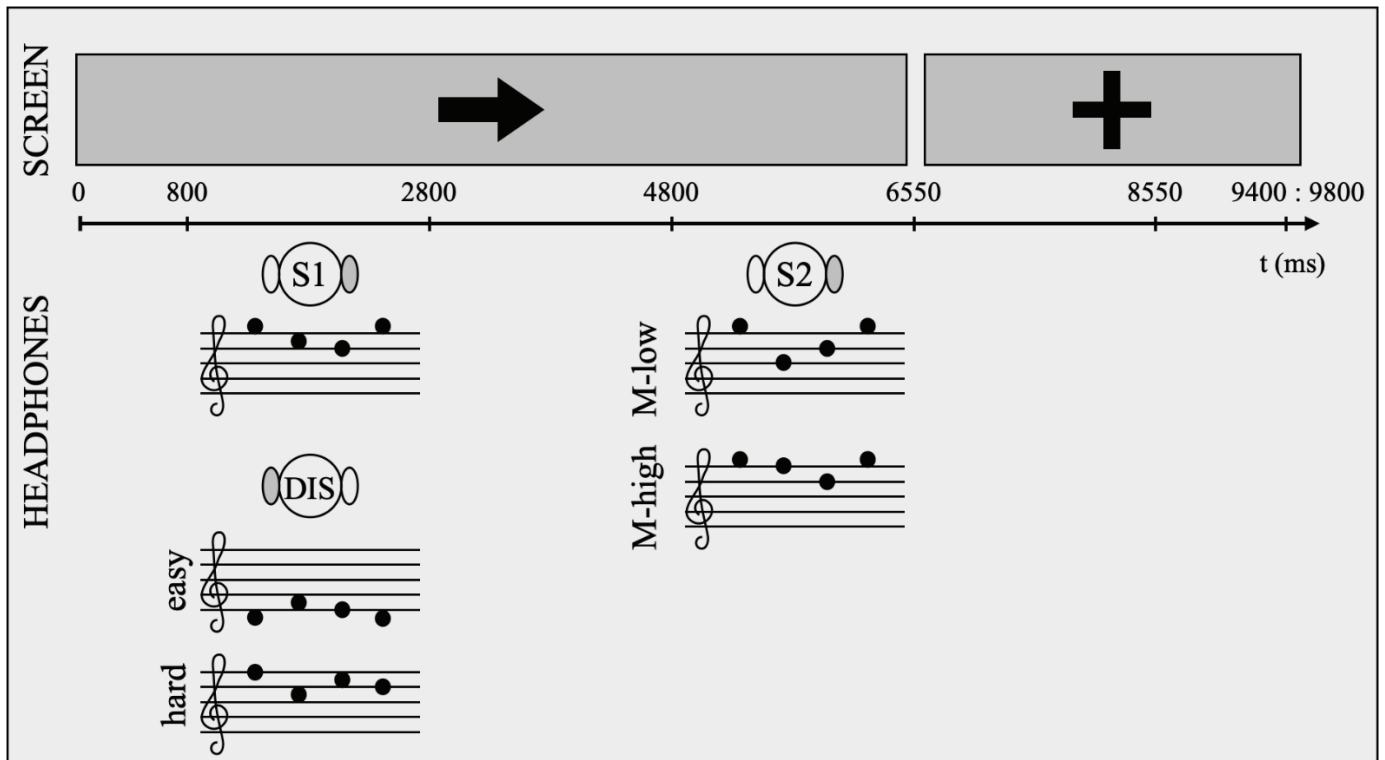


Figure 27 - Trial design.

Procedure

First, participants have to fill in questionnaire and ethics. Then, they are installed in the MEG in a seated position. All stimuli are delivered using Presentation software (Neurobehavioral Systems, Albany, CA, USA). Sounds are delivered through air-conducting plastic ear tubes. They undergo a volume calibration so that the auditory stimuli are easy to hear (hearing threshold +20 dB). As a first step, we record 5 minutes of resting state MEG data while the subjects are instructed to fixate the cross displayed on the screen in front of them, to relax and not to fall asleep. We control a posteriori the absence of reasoning or planning during these 5 minutes by asking them what they thought about.

They then perform the main task. They are instructed to answer as accurately as possible and to keep fixating the cross during each trial. Prior to the actual task, they perform two short training blocks (12 trials) for each memory load. Training melodies (S1, DIS and S2) are specific to the training sessions. Finally, they perform the ten experimental blocks (48 trials each), 5 under each memory load (low or high). They are aware of the difficulty of the memory task but not of the difficulty of the distractors, which is randomized within one block. Trials last 8800ms, leading to six-minute-long memory blocks. Immediately after the MEG experiment, the subjects underwent a 10-minutes long structural T1-weighted MR imaging.

Balancing – within blocks

Each block contains 48 trials. All the combinations of ear of interest (Left or Right), distractor difficulty (easy DIS or hard DIS), associated answer (same or different) are equiprobable within block (6 trials/block each). For each combination with an expected answer “different”, the direction of the change is equiprobably ascending or descending in frequency (3 trials/block each).

This within-block balancing allows to control for side, expected answer, and change direction.

Balancing – between blocks

For a given S1 melody, the answer, the direction of the change in S2 when different, the level of DIS difficulty, and the side of presentation are balanced across blocks.

Blocks order are balanced between subjects (Latin square). For half of the participants, melodies S1 and DIS are inverted and become respectively DIS and S1. Association between one S1 melody and another DIS melody changes across participants, enabling us to limit the impact in the results from any unfortunate easy or difficult match.

Analysis

Trial rejection

Trials in which participants gave no answer, several answers, or did answer at an inappropriate moment (i.e. outside of the indicated period) are excluded from analysis. Average number of trials per participant after this exclusion is 476 trials +/- std 4 (out of 480).

Measurements

dprime (d') is the difference between normalized "Hits" and normalized "False alarms". Hits are the proportion of correct "different" answer over all "different" trials, and False alarms are the proportion of incorrect "different" answer over all "same" trials. Criterion (c) indicates the response bias. Positive values indicate the tendency of answering "same" and negative values reflect the tendency of answering "different". Median Reaction Times (RTs) are computed out of correctly answered trials and correspond to the time between the end of the sound (*i.e.* S1+DIS in the perception blocks, and S2 in the memory blocks irrespective of the change position in S2) and the button press.

Group comparison

We compared results (d', RT) between groups thanks to a Bayesian repeated-measure ANOVA with MEMORYload (memory load, two levels: low, high), DISdiff (difficulty of the DIStractor, two levels: easy DIS, hard DIS) as within-participant factors, and GROUP (two levels: LDR, HDR) as a between-participant factor. Post-hoc Bayesian t-tests were computed to investigate interactions contributing to the best model: between easyDIS and hardDIS for LDR and HDR separately, and between easyDIS and hardDIS under low and high memory load separately.

DIS difficulty cost (easyDIS minus hardDIS) and load cost (low minus high load) were computed in terms of d'. To assess the effect of dream recall frequency on attentional filtering and memory load, planned Bayesian t-tests have been computed to compare groups for each cost (DIS difficulty cost, load cost) and to compare costs for each group (LDR, HDR).

We reported Bayes Factor (BF_{10}) as a relative measure of evidence (compared to the null model). To interpret the strength of evidence against the null model, we considered a BF between 1 and 3 as weak evidence, a BF between 3 and 10 as positive evidence, a BF between 10 and 100 as strong evidence and a BF higher than 100 as a decisive evidence (Lee & Wagenmakers, 2014). Similarly, to interpret the strength of evidence in favour of the null model, we considered a BF between 0.33 and 1 as weak evidence, a BF between 0.01 and 0.33 as positive evidence, a BF between 0.001 and 0.01 as strong evidence and a BF lower than 0.001 as a decisive evidence.

Additionally, we report for each factor and interaction the $BF_{inclusion}$ that compares models that contain the effect to equivalent models stripped of the effect and was considered as a relative measure of evidence supporting the inclusion of a factor.

All statistical analyses were conducted using the software JASP (Wagenmakers et al., 2018).

Results

Demographics and neuropsychological data

Bayesian t-tests confirm that the two groups were matched in school education, age, laterality and gender ($0.4 < BF_{10} < 0.8$; see Table 2). Also, as expected, there is decisive evidence ($BF_{10} = 5.4e+7$) for a difference of dream recall frequency between groups. There is only weak evidence for any difference in STAI, BFI, PQSI and GAUT measures between the groups ($0.4 < BF_{10} < 1.7$; see Table 2).

Behavioral results

For d' , (see Figure 28, Sup.Table 44), the best model explaining data in LR and HR is the model with the factors GROUP, MEMORYload, DISdiff, the interaction between MEMORYload and DISdiff and the interaction between GROUP and DISdiff ($BF_{10} = 1.8e+23$). There is decisive evidence for an effect of GROUP ($BF_{inclusion} = 2.1e+4$), MEMORYload ($BF_{inclusion} = 1.4e+20$) and DISdiff ($BF_{inclusion} = 7.5e+6$), positive evidence for an effect of the interaction between MEMORYload and DISdiff ($BF_{inclusion} = 4.3$), and weak evidence for an effect of the interaction between GROUP and DISdiff ($BF_{inclusion} = 1.3$) (see Sup.Table 45).

Post-hoc tests reveal decisive evidence for a difference between easy and hardDIS conditions under low memory load ($BF_{10} = 18462.4$) and strong evidence for a difference between easy and hard DIS conditions under high memory load ($BF_{10} = 56.5$). d' are higher for easy-to-ignore distractors (easyDIS) compared to hard-to-ignore distracting melodies (hardDIS), and this difference is higher under low load compared to high load.

Post-hoc tests reveal weak evidence for a difference between groups under easyDIS ($BF_{10} = 2.6$) and decisive evidence for a difference between groups under hardDIS ($BF_{10} = 980.7$). d' are higher for low dream recallers (LDR) compared to high dream recallers (HDR), and this difference is higher for hardDIS compared to easyDIS.

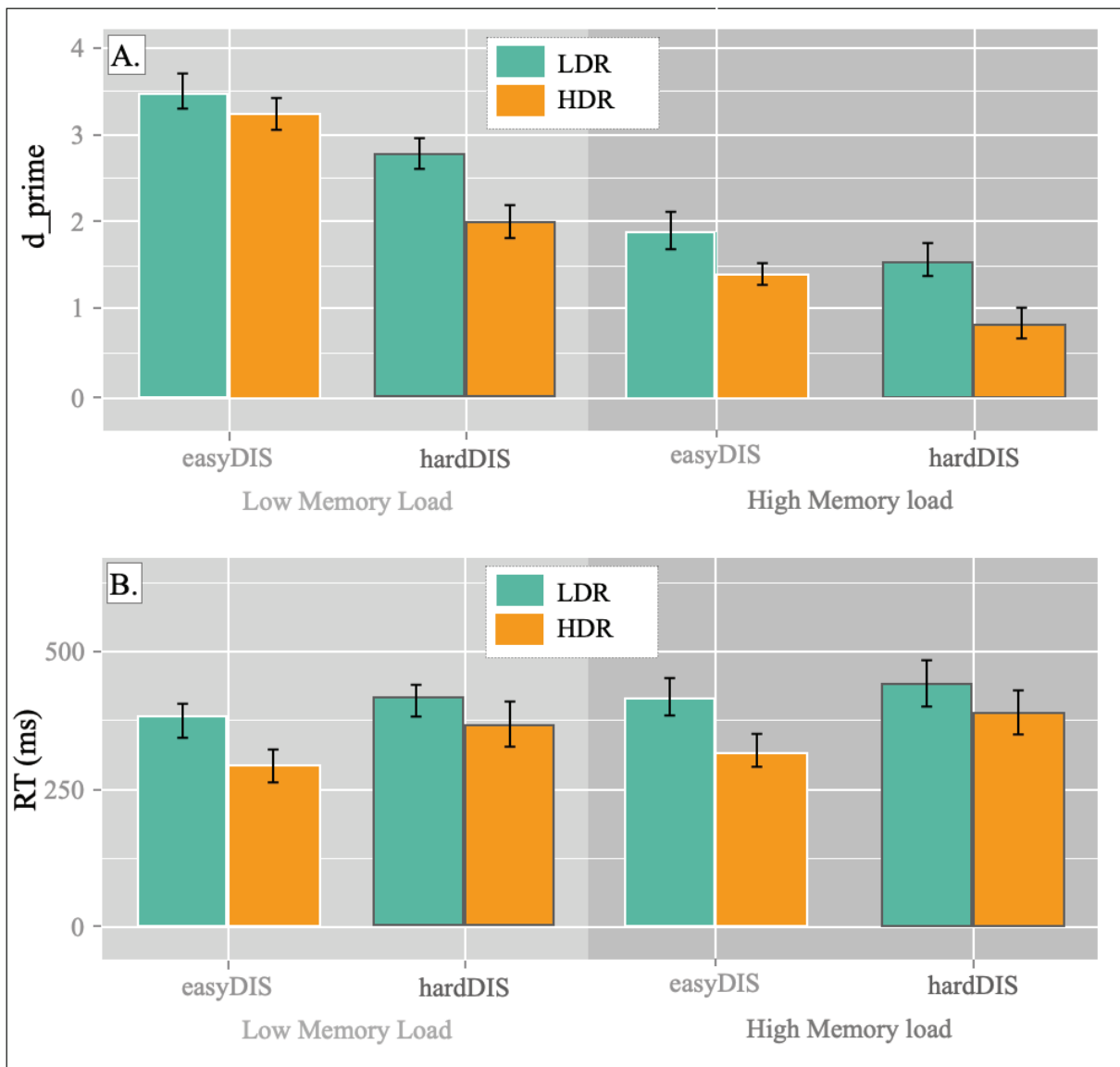


Figure 28 - Behavioral results of low and high dream recallers. Effects of the distraction difficulty and task load on d' -primes (A.) and RTs (B.) for both groups separately.

In terms of distractor difficulty and memory load costs on d' (see Figure 29), there is weak evidence for a difference of distractor difficulty cost between groups ($BF_{10}=1.1$) and weak evidence for no difference of memory load cost between groups ($BF_{10}=0.4$).

There is respectively strong and positive evidence towards a difference between distractor difficulty and memory load costs on d' in both LDR ($BF_{10}=87.2$) and HDR ($BF_{10}=4.0$) groups. Overall, low dream recallers tend to have smaller distractor difficulty cost than high dream recallers, and both groups tend to have similar memory load cost.

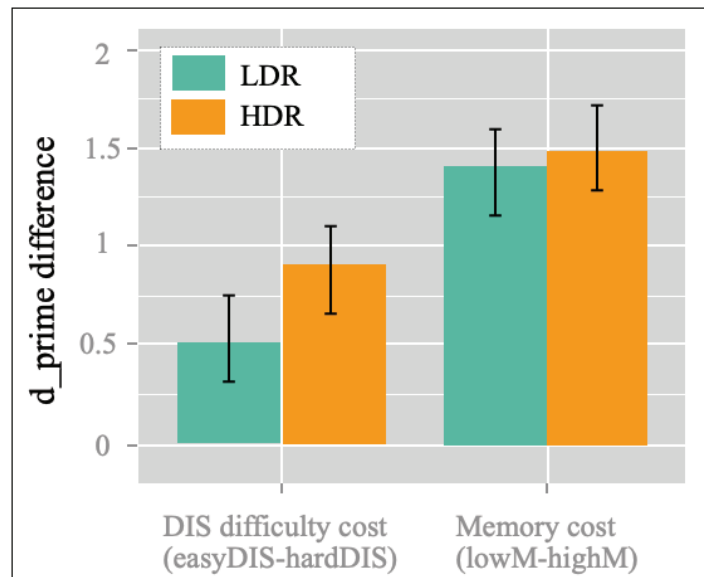


Figure 29 - Group comparison for distractor difficulty and memory load costs on d' . Distractor difficulty cost is the difference between condition easy- and hard-to-ignore distractors. Memory load cost is the difference between low and high memory load.

For the criterion, in agreement with previous studies using delayed-matching-to-sample tests, there is weak to strong evidence for positive c values (see Sup.Table 50), underlining that participants tended to miss differences between melodies.

The best model explaining criterion data (see Sup.Table 46) is composed of the factors MEMORYload, DISdiff, ($BF_{10}=2.2e+8$). There is decisive evidence for an effect of MEMORYload ($BF_{inclusion}=1.9e+7$) and DISdiff ($BF_{inclusion}=92.8$) (see Sup.Table 47).

For the RTs, the best model explaining the results is the one with GROUP and DISdiff ($BF_{10}=9.2e+4$; see Sup.Table 48). There is decisive evidence for GROUP effect ($BF_{inclusion}=2.9e+4$) and positive evidence for DISdiff effect ($BF_{inclusion}=9.4$) (see Sup.Table 49). RTs are longer for hard DIS compared to easy DIS, they are longer for low- compared to high-frequency dream recallers.

Discussion

Low dream frequency recallers are significantly slower and more accurate than high frequency dream recallers in the MEMAT task. There is greater evidence for a difference of distractor difficulty cost than for a difference of memory cost between groups. There is greater evidence for a difference between the distractor difficulty cost and the memory cost for low frequency dream recallers than for high frequency dream recallers.

Our results underline no significant difference in neuropsychological tests between low and high frequency dream recallers. However, several studies indicate differences in terms of personality or creativity between these groups reports (Hartmann et al., 1998; Schredl et al., 1997). Compared to such studies, our group of participants appear to be of a much smaller size, which could explain this difference.

The index generated for the Guilford creativity test, for example, depends largely on the number of participants included, as the notation depends on the overall proportions of the entire group. However, even the difference between groups is not significant, numerical tendency indicates a greater creativity score for the high frequency dream recallers, which is coherent with previous results acquired in the lab (Vallat&Ruby, in prep.).

Even not significant, high dream recallers seem to be more anxious than low dream recallers (see STAI scores), and to have a greater BFI opening score. These tendencies can suggest predispositions for more susceptibility to environmental stimuli.

The only weak evidence towards a difference between groups for neuropsychological tests concerns the STAI index of nervousity, which can be related to impulsivity; high dream recallers tend to have a higher score of nervousity than low dream recallers.

Across groups, the behavioral results of this new study are consistent with the results of non-musicians tested in the first behavioral study (see Article 1, SHARED COGNITIVE RESOURCES BETWEEN MEMORY AND ATTENTION DURING SOUND SEQUENCE ENCODING): there is an effect of memory load and distractor difficulty upon d' , with better performances for low compared to high memory load, and better performances for easy- compared to hard-to ignore distractors. Furthermore, the interaction between memory load and distractor difficulty is again present, with greater difference between easy and hard to ignore distractors under low memory load than under high memory load. Again, the reaction times are not affected by the memory load, but only by the difficulty of the attentional task, with greater reaction times for hard- compared to easy-to-ignore distractors.

When comparing groups, it appears that low- and high-dream recallers have two different strategies when performing the MEMAT task. Low frequency dream recallers are slower, but more accurate than high frequency dream recallers. Furthermore, low frequency dream recallers are less impacted than the high frequency dream recallers by harder-to-ignore distractors. The distractor difficulty cost is reduced compared to the memory load cost in both groups, even if this difference seems to be accentuated for low frequency dream recallers.

Overall, low frequency dream recallers appear to have a more conservative strategy, taking more time to answer but being less distracted, especially with harder to ignore distracting melodies, in opposition to high frequency dream recallers who are somewhat impulsive. This result is consistent with previous findings claiming that low dream recallers are more resistant to salient distracting sounds, and that high dream recallers are more sensitive to their external environment (Eichenlaub et al., 2014; Escera et al., 2003; Garcia-Garcia et al., 2008).

These behavioral differences are likely to be mirrored in electrophysiological recordings. Indeed, magnetoencephalography recordings have been made during the task, and we plan to investigate the impacts of group, DISdiff and MEMORYload effects on them. We expect differences between groups, that would reflect different attentional treatments. It would be interesting to test whether this hypothetical result would be driven by more filtering of the distractors, more facilitation of the targets, or both.

In terms of oscillatory process, we would expect more alpha desynchronization in the auditory areas, and more alpha synchronization in the visual areas for low compared to high frequency dream recallers. Finally, if attention and memory share resources during encoding, these effects should impact memory processes, and the interaction between DISdiff and MEMORYload needs to be deeply investigated as well in MEG recordings.

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Supplementary data

ANOVA on d' with factors GROUP, MEMORYload and DISdiff

	Models	P(M)	P(M data)	BF_M	BF₁₀	error %
d'	Null model (incl. subject)	0.053	1.7e -24	3.1e-23	1.000	X
	GROUP + MEMORYload + DISdiff + GROUP*DISdiff + MEMORYload*DISdiff	0.053	0.3	8.4	1.9e +23	3.9
	GROUP + MEMORYload + DISdiff + MEMORYload*DISdiff	0.053	0.2	6.0	1.5e +23	3.4
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload + GROUP*DISdiff + MEMORYload*DISdiff	0.053	0.1	2.4	6.9e +22	13.7
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload + MEMORYload*DISdiff	0.053	0.1	1.5	4.5e +22	3.2
	GROUP + MEMORYload + DISdiff + GROUP * DISdiff	0.053	0.1	1.4	4.3e +22	2.3
	GROUP +MEMORYload + DISdiff + GROUP*MEMORYload + GROUP*DISdiff + MEMORYload*DISdiff + GROUP*MEMORYload*DISdiff	0.053	0.1	1.2	3.8e +22	21.2
	GROUP + MEMORYload + DISdiff	0.053	0.1	1.1	3.4e +22	2.9
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload + GROUP*DISdiff	0.053	0.0	0.5	1.5e +22	6.8
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload	0.053	0.0	0.4	1.3e +22	5.3
	MEMORYload + DISdiff + MEMORYload*DISdiff	0.053	9.7e-6	1.8e-4	5.8e +18	2.85
	MEMORYload + DISdiff	0.053	4.7e-6	8.5e-5	2.8e +18	1.7
	GROUP + MEMORYload	0.053	7.8e-9	1.4e-7	4.6e +15	1.34
	GROUP + MEMORYload + GROUP*MEMORYload	0.053	2.4e-9	4.3 -8	1.4e +15	1.9
	MEMORYload	0.053	2.7e -11	4.9e-10	1.6e +13	0.9
	GROUP + DISdiff	0.053	5.5e -22	10.0e-21	327.9	1.6
	GROUP + DISdiff + GROUP*DISdiff	0.053	2.3e -22	4.2e-21	138.9	1.8
	DISdiff	0.053	8.1e -23	1.5e-21	47.7	1.4
	GROUP	0.053	7.6e -24	1.4e-22	4.5	1.1

Sup.Table 44 - Bayesian ANOVA results for d' analysis (factors: GROUP, MEMORYload, DISdiff).

d'	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	GROUP	0.263	0.3	21154.2
	MEMORYload	0.263	0.1	1.5e +20
	DISdiff	0.263	0.1	7.7e +6
	GROUP * MEMORYload	0.263	0.2	0.3
	GROUP * DISdiff	0.263	0.5	1.3
	MEMORYload * DISdiff	0.263	0.8	4.3
	GROUP * MEMORYload * DISdiff	0.053	0.1	0.5

Sup. Table 45 - Analysis of effects for the Bayesian ANOVA on d' (factors: GROUP, MEMORYload, DISdiff).

ANOVA on criterion with factors GROUP, MEMORYload and DISdiff

	Models	P(M)	P(M data)	BF_M	BF₁₀	error %
c	Null model (incl. subject)	0.053	1.5e-9	2.7e-8	1.0	
	MEMORYload + DISdiff	0.053	0.3	8.8	2.2e+8	2.4
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.053	0.3	8.2	2.1e+8	2.5
	GROUP + MEMORYload + DISdiff	0.053	0.1	1.8	6.0e+7	2.5
	GROUP + MEMORYload + DISdiff + MEMORYload * DISdiff	0.053	0.1	1.7	5.8e+7	3.4
	GROUP + MEMORYload + DISdiff + GROUP * DISdiff	0.053	0.0	0.8	2.9e+7	3.2
	GROUP + MEMORYload + DISdiff + GROUP*DISdiff + MEMORYload*DISdiff	0.053	0.0	0.8	2.8e+7	4.1
	GROUP + MEMORYload + DISdiff + GROUP * MEMORYload	0.053	0.0	0.5	2.0e+7	3.0
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload + MEMORYload*DISdiff	0.053	0.0	0.5	1.8e+7	2.6
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload + GROUP*DISdiff	0.053	0.0	0.2	9.0e+6	4.2
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload + GROUP*DISdiff + MEMORYload*DISdiff	0.053	0.0	0.2	9.0e+6	5.6
	GROUP + MEMORYload + DISdiff + GROUP*MEMORYload + GROUP * DISdiff + MEMORYload*DISdiff + GROUP*MEMORYload * DISdiff	0.053	0.0	0.1	4.4e+6	7.6
	MEMORYload	0.053	0.0	0.1	2.4e+6	2.3
	GROUP + MEMORYload	0.053	9.4e-4	0.0	623570.1	2.0
	GROUP + MEMORYload + GROUP * MEMORYload	0.053	3.0e-4	0.0	196391.0	1.8
	DISdiff	0.053	1.6e-8	2.9e-7	10.6	0.8
	GROUP + DISdiff	0.053	4.2e-9	7.6e-8	2.8	3.4
	GROUP + DISdiff + GROUP * DISdiff	0.053	1.6e-9	2.9e-8	1.1	2.8
	GROUP	0.053	3.8e-10	6.9e-9	0.3	1.8

Sup. Table 46 - Bayesian ANOVA results for the criterion analysis (factors: GROUP, MEMORYload, DISdiff).

c	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	GROUP	0.263	0.2	0.3
	MEMORYload	0.263	0.5	2.0e +7
	DISdiff	0.263	0.4	95.8
	GROUP * MEMORYload	0.263	0.1	0.3
	GROUP * DISdiff	0.263	0.1	0.4
	MEMORYload * DISdiff	0.263	0.5	1.0
	GROUP * MEMORYload * DISdiff	0.053	0.0	0.9

Sup. Table 47 - Analysis of effects for the Bayesian ANOVA on c (factors: GROUP, MEMORYload, DISdiff).

ANOVA on RT with factors GROUP, MEMORYload and DISdiff

	Models	P(M)	P(M data)	BF_M	BF₁₀	error %
RT	Null model (incl. subject)	0.053	0.0	0.0	1.0	
	GROUP + DISdiff	0.053	0.3	7.5	97188.7	2.7
	GROUP + MEMORYload + DISdiff	0.053	0.2	4.0	60003.5	1.8
	GROUP + DISdiff + GROUP * DISdiff	0.053	0.1	3.1	48659.8	2.1
	GROUP + MEMORYload + DISdiff + GROUP * DISdiff	0.053	0.1	2.0	32759.4	3.5
	GROUP + MEMORYload + DISdiff + GROUP * MEMORYload	0.053	0.1	1.2	21330.3	8.0
	GROUP + MEMORYload + DISdiff + MEMORYload * DISdiff	0.053	0.1	1.1	19447.3	2.3
	GROUP + MEMORYload + DISdiff + GROUP * DISdiff + MEMORYload * DISdiff	0.053	0.0	0.6	10916.4	2.8
	GROUP	0.053	0.0	0.6	10865.9	2.0
	GROUP + MEMORYload + DISdiff + GROUP * MEMORYload + GROUP * DISdiff	0.053	0.0	0.5	9622.1	2.7
	GROUP + MEMORYload + DISdiff + GROUP * MEMORYload + MEMORYload * DISdiff	0.053	0.0	0.4	7878.3	19.6
	GROUP + MEMORYload	0.053	0.0	0.3	6256.6	2.0
	GROUP + MEMORYload + DISdiff + GROUP * MEMORYload + GROUP * DISdiff + MEMORYload * DISdiff	0.053	0.0	0.2	2823.2	3.4
	GROUP + MEMORYload + GROUP * MEMORYload	0.053	0.0	0.1	2187.1	4.9
	GROUP + MEMORYload + DISdiff + GROUP * MEMORYload + GROUP * DISdiff + MEMORYload * DISdiff + GROUP * MEMORYload * DISdiff	0.053	0.0	0.1	1332.5	9.7
	DISdiff	0.053	0.0	0.0	3.1	1.2
	MEMORYload + DISdiff	0.053	0.0	0.0	1.5	1.3
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.053	0.0	0.0	0.5	7.7
	MEMORYload	0.053	0.0	0.0	0.5	1.4

Sup. Table 48 - Bayesian ANOVA results for the analysis of RTs (factors: GROUP, MEMORYload, DISdiff).

RT	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	GROUP	0.263	0.56	29594.6
	MEMORYload	0.263	0.3	0.6
	DISdiff	0.263	0.5	9.2
	GROUP * MEMORYload	0.263	0.1	0.3
	GROUP * DISdiff	0.263	0.3	0.5
	MEMORYload * DISdiff	0.263	0.1	0.3
	GROUP * MEMORYload * DISdiff	0.053	0.0	0.5

*Sup. Table 49 - Analysis of effects for the Bayesian ANOVA on RTs (factors: **GROUP**, **MEMORYload**, **DISdiff**).*

Criterion data: BF_{10} are extracted from comparison to zero (Bayesian one-sample t-test)

			MEMAT - MEG		
			mean	SD	BF_{10}
Low Dream Recallers	Low Memory	Easy DIS	0.1	0.4	0.5
		Hard DIS	0.0	0.4	0.3
	High Memory	Easy DIS	0.7	0.5	71.0
		Hard DIS	0.5	0.3	76.1
High Dream Recallers	Low Memory	Easy DIS	0.2	0.3	3.0
		Hard DIS	0.1	0.3	0.4
	High Memory	Easy DIS	0.8	0.4	517.2
		Hard DIS	0.4	0.3	32.4

Sup. Table 50 - Criterion data (mean, SD: standard deviation) for all conditions and groups (GROUP, MEMORYload and DISdiff). BF_{10} correspond to Bayesian one-sample test comparison to zero.

**NEURAL CORRELATES OF THE INTERACTION BETWEEN
AUDITORY NON-VERBAL
SELECTIVE ATTENTION AND WORKING MEMORY
DURING ENCODING**

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The following results are preliminary.

Introduction

MEMAT paradigm was designed to be used in conjunction with electrophysiology recordings to tackle the cerebral basis of selective attention, working memory, and their interaction, during sound sequence encoding. The last part of this PhD work is dedicated to the results obtained thanks to magnetoencephalography recordings.

As we observed an effect of both memory load and distractor difficulty on the behavioral results in previous sections, we expect these results to be reflected in brain activity. As presented in the general hypotheses (see GENERAL HYPOTHESES), we expect memory load to impact the sustained evoked responses, and attention manipulation to impact alpha oscillatory activities. Both of them should have an impact on obligatory evoked responses such as the N1. Finally, we search for interactions between working memory and selective attention processes in these measures.

Methods

Participants, stimuli, paradigm, procedure and behavioral analysis are identical to the one presented in the previous article (article 2, see WORKING MEMORY AND SELECTIVE ATTENTION IN LOW VERSUS HIGH FREQUENCY DREAM RECALLERS). To jump directly to the supplementary methods specific to this article, go to *MRI Data* (p203).

Participants

Twenty-two non-musician participants (20 right-handed, 11 men and 11 women, aged 20-33 years, mean 23.8 +/-std 3.3) participated in the experiment. 2 participants were left-handed, the others were right-handed. Participants were considered as non-musicians when they practiced less than 1 year of instrument or singing outside compulsory educative programs (mean 0.1 year of music education, std=0.4). The average number of years of education was 15.5 years (+/- std 2.0).

All participants were free from neurological or psychiatric disorder and had normal hearing and normal vision. All subjects gave their written informed consent to participate. Experimental procedures were approved by the appropriate national ethics committee.

Stimuli

240 four-sounds-long melodies were created thanks to combinations of eight-harmonic synthetic sounds from the C major scale, spanning four octaves between 65 and 1046Hz. The maximal interval between any two sounds of a melody is 7 semi-tones. Sounds are 250-ms long and the interval between sounds (offset to onset) is 250 milliseconds.

In each melody, there is no consecutive identical sounds. Every melody contains at least an ascending and a descending interval.

Paradigm

Attention manipulation

The melody of interest (S1) and the distracting melody (DIS) melodies are nested, but not played simultaneously. S1 is played in the indicated ear (see below), and DIS is played in the other ear, each tone one after the other. The first sound to be played is the first tone of S1, and the last tone to be played is the last tone of DIS.

The DIS melodies can be rather easy (easy DIS) or hard (hard DIS) to filter. An easy DIS melody is composed of sounds in a frequency range 5-tone-higher (or lower) than the corresponding S1 melody frequency range. A hard DIS melody frequency range is the same than the corresponding S1 melody frequency range. DIS melodies are constructed with the same rules as for the S1 melodies, as described above.

Memory task

For each trial (see Figure 30), the participant is informed of the ear of interest by an arrow (all visual contents are seven-centimeter-wide black elements displayed individually at the center of a white screen). 800ms after the arrow presentation onset, S1 and DIS are played in the ear of interest and in the other ear, respectively. After a 2000-ms pause, during which a cross is displayed on the screen, the melody (S2) to compare to S1 is played in the ear of interest. The participant has then 2000 ms to answer to the question “Is S2 identical or different from S1?”. When S2 differs from S1, only one sound out of four differs, and it can be either the second, third, or fourth one, never the first one which would be too salient. The answer period starts at the end of the S2 melody.

In the low memory load task (low-M), when S2 differs from S1, one sound is replaced by another which is 4 tones apart (ascending or descending) and induces a change in the melody contour. In the high memory load task (high-M), when S2 differs from S1, the changed sound differs from the original one only by 1 tone and does not induce a change in the melody contour.

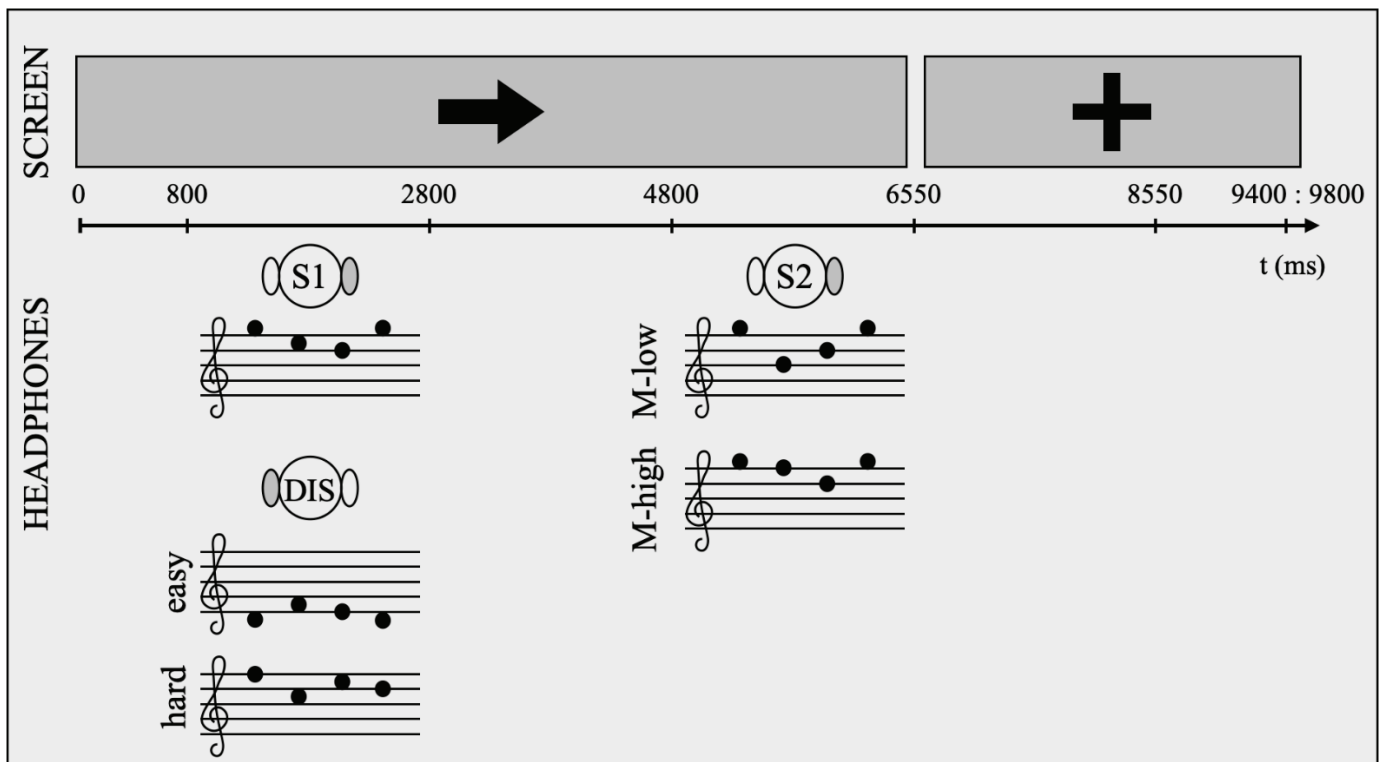


Figure 30 - Trial design.

Procedure

First, participants have to fill in questionnaires and ethics. Then, they are installed in the MEG in a seated position. All stimuli are delivered using Presentation software (Neurobehavioral Systems, Albany, CA, USA). Sounds are delivered through air-conducting plastic ear tubes. They undergo a volume calibration so that the auditory stimuli are easy to hear (hearing threshold +20 dB). As a first step, we record 5 minutes of resting state while the subjects are instructed to fixate the cross displayed on the screen in front of them, to relax and not to fall asleep. We control a posteriori the absence of reasoning or planning during these 5 minutes by asking them what they thought about.

They then perform the main task. They are instructed to answer as accurately as possible and to keep fixating the cross during each trial. Prior to the actual task, they perform two short training blocks (12 trials) for each memory load. Training melodies (S1, DIS and S2) are specific to the training sessions. Finally, they perform the ten experimental blocks (48 trials each), 5 under each memory load (low or high). They are aware of the difficulty of the memory task but not of the difficulty of the distractors, which is mixed within one block. Trials last 8800ms, leading to six-minute-long memory blocks. Immediately after the MEG experiment, the subjects underwent a 10-minutes long structural T1-weighted MR imaging.

Balancing – within blocks

Each block contains 48 trials. All the combinations of ear of interest (Left or Right), distractor difficulty (easy DIS or hard DIS), associated answer (same or different) are equiprobable within block and subject (6 trials/block each). For each combination with an expected answer “different”, the direction of the change is equiprobable to be ascendant or descendant frequencies (3 trials/block each).

This within-block balancing allows to control for side, answer and change direction.

Balancing – between blocks

For a given S1 melody, the answer, the direction of the change in S2 when different, the level of DIS difficulty, and the side of presentation are balanced across blocks.

Blocks order are balanced between subjects (Latin square). For half of the participants, melodies S1 and DIS are inverted and become respectively DIS and S1.

Association between one S1 melody and another DIS melody changes across participants, enabling us to limit the impact in the results from any unfortunate easy or difficult match.

Behavioral Data

Trial rejection

Trials in which participants gave no answer, several answers, or did answer at an inappropriate moment (i.e. outside of the indicated period) are excluded from analysis. Average number of trials per participant after this exclusion is 476 trials +/- std 4 (out of 480 trials).

Measurements

dprime (d') is the difference between normalized “Hits” and normalized “False alarms”. Hits are the proportion of correct “different” answer over all “different” trials, and False alarms are the proportion of incorrect “different” answer over all “same” trials.

Criterion (c) indicates the response bias. Positive values indicate the tendency of answering “same” and negative values reflect the tendency of answering “different”.

Median Reaction Times (RTs) are computed out of correctly answered trials and correspond to the time between the end of the sound (i.e. S1+DIS in the perception blocks, and S2 in the memory blocks irrespective of the change position in S2) and the button press.

Main statistical analyses

Criterion for each main factor combination (MEMORYload x DISdiff) were submitted to a Bayesian one-sample t-test comparison to zero.

d', RTs and criterion were submitted to a Bayesian repeated-measure ANOVA with MEMORYload (difficulty of the task, two levels: low, high), DISdiff (difficulty of the

DIStractor, two levels: easy DIS, hard DIS) as within-participant factors. Post-hoc comparisons for significant effects or interactions were conducted using Bayesian t-tests.

We reported Bayes Factor (BF_{10}) as a relative measure of evidence (compared to the null model). To interpret the strength of evidence against the null model, we considered a BF between 1 and 3 as weak evidence, a BF between 3 and 10 as positive evidence, a BF between 10 and 100 as strong evidence and a BF higher than 100 as a decisive evidence (Lee & Wagenmakers, 2014). Similarly, to interpret the strength of evidence in favor of the null model, we considered a BF between 0.33 and 1 as weak evidence, a BF between 0.01 and 0.33 as positive evidence, a BF between 0.001 and 0.01 as strong evidence and a BF lower than 0.001 as a decisive evidence.

Additionally, we report for each factor and interaction the BF inclusion that compares models that contain the effect to equivalent models stripped of the effect and was considered as a relative measure of evidence supporting the inclusion of a factor.

All statistical analyses were conducted using the software JASP (Wagenmakers et al., 2018).

MRI Data

Recordings

For each participant, a T1 weighted 3D MRI was obtained using a 1.5T or 3T whole-body scanner (Magnetom Siemens Erlangen, Germany). At the end of MEG session, locations of the nasion and the two preauricular points were marked using fiducials markers visible on the T1 acquisitions. The T1 images were used for reconstruction of individual head shapes to create forward models for the source reconstruction procedures.

Analysis

For the source reconstruction of the event-related fields (ERFs): We performed the segmentation of the T1 MRI with the FreeSurfer software package (Fischl, 2012) (<http://surfer.nmr.mgh.harvard.edu>). Segmentation were visually inspected and then imported (15002 vertices) in the Brainstorm toolbox.

For the source reconstruction of the oscillations: the processing of the T1 MRI was performed using the CTF's software (CTF Systems Inc., VSM Medtech Inc., Vancouver, Canada). For each participant, an anatomically realistic single shell headmodel based on the cortical surface was generated from individual head shapes (Nolte, 2003).

MEG Data Analysis

MEG recordings

MEG data were continuously recorded using a 275-channel whole-head axial gradiometer system (CTF-275 by VSM MedTech Inc., Vancouver, Canada) with a sampling rate of 600Hz. Data were online filtered with a bandpass filter 0.016-150Hz and a first-order spatial gradient noise cancellation was applied. Head movements were continuously monitored using 3 coils placed at the nasion and the two preauricular points. Note that the MEG system is within a magnetically shielded recording booth.

Pre-processing

The recorded signal was rejected when head movements exceed the threshold of +/-1cm around the median position.

Blinks, saccades and heartbeats were removed from the signal thanks to an Independent Component Analysis (ICA) which was computed on the band-pass filtered signal (0.5-45Hz). Eye-movements and heartbeat related components were determined by visual inspection of component topographies and time courses and removed through an ICA inverse transformation applied to the non-filtered signal.

Data segments contaminated with muscular activity or sensor jumps were excluded using a threshold of 2.5 and 10 picoTesla, respectively. For all participants, more than 95% of trials remained in the analyses after rejection.

ERF sensor-level analysis

ERFs on sensors were computed thanks to the software ELAN developed at the Lyon Neuroscience Research Center (elan.lyon@inserm.fr; Aguera et al., 2011). Band-stop filters were applied to remove the 50Hz power-line artifact and its harmonics (47-53; 97-103; and 147-153 Hz) on the ICA-corrected signal. Then for each condition, ERFs from -300 to 8000ms around the onset of S1 were obtained by averaging band-stopped ICA-corrected MEG data locked to the onset of S1. All but artefact-rejected trials were included in the computation of the ERFs, depending only on the experimental conditions. The ERFs were then filtered either with a low-pass filter of 2Hz, either with a band-pass filter from 2 to 30Hz, in order to study slow (sustained) and transient evoked responses, respectively (see Figure 31. A baseline, from -250ms to 0ms before the onset of S1, was subtracted to the ERFs. Grand-average ERF is obtained by averaging the same computed ERF across all 22 subjects.

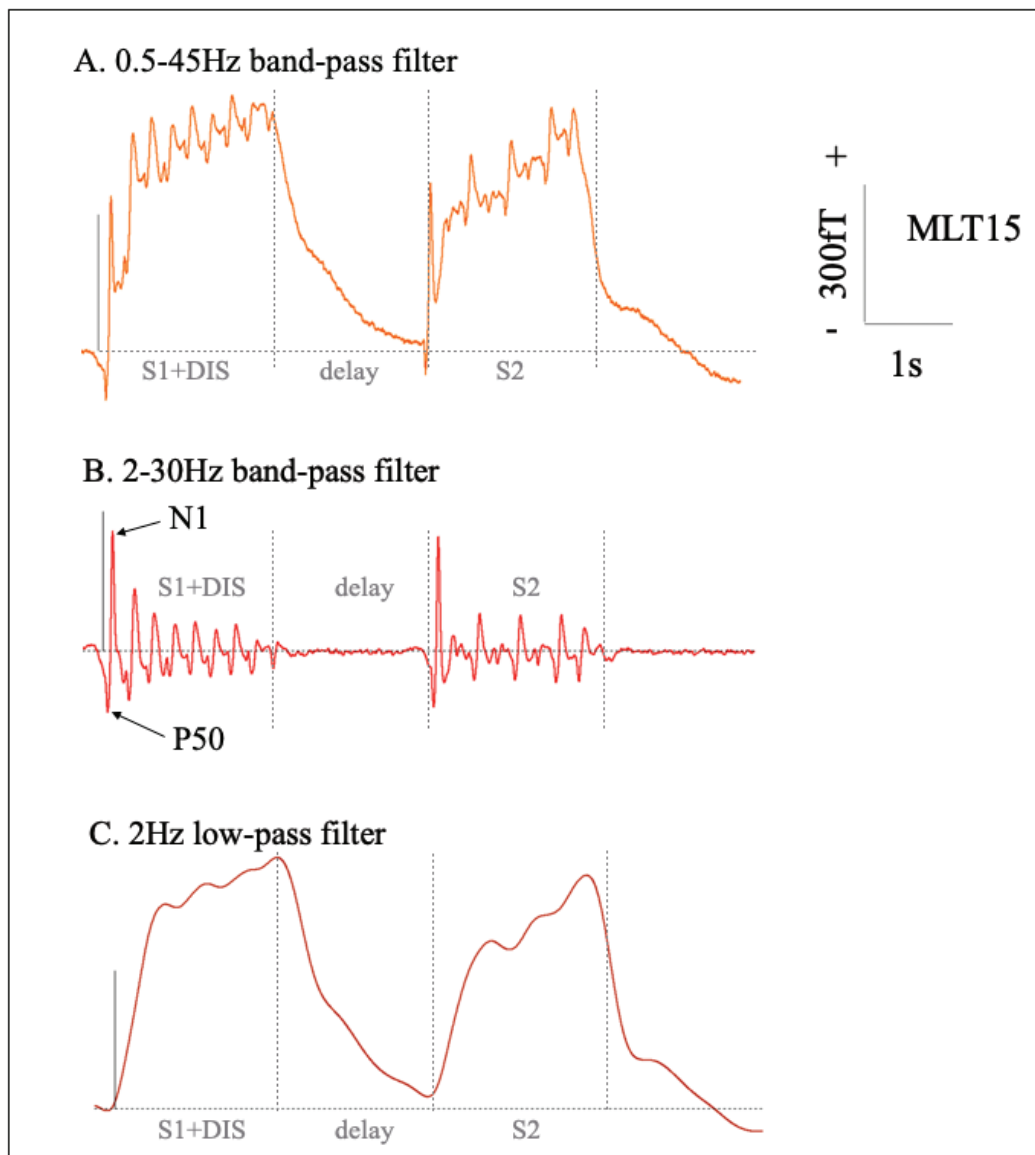


Figure 31 – Grand average of a left temporal MEG sensor (MLT15) for a trial time window (-250ms to 8000ms), for all participants, collapsed across conditions. (A.) Event-related fields filtered with a 0.5-45Hz band-pass filter, with a baseline applied from -250 to 0ms relative to the onset of S1+DIS. (B.) Event-related fields filtered with a 2-30Hz band-pass filter to uncover transient evoked responses, same baseline as A. (C.) Event related fields filtered with a 2Hz low-pass filter to uncover sustained evoked responses, same baseline as A.

Because of saliency effects on the first note we only further analyzed the averaged ERFs for the second, third, and fourth sounds of the melodies, separately for S1 and DIS, to explore transient evoked responses to S1 and DIS sounds, respectively. The averaged time windows are then 500:750ms, 1000:1250ms, 1500ms:1750ms for the S1, and 750:1000ms, 1250:1500ms, 1750:2000ms for the DIS.

ERF source reconstruction

The white-matter / grey-matter boundary segmented by FreeSurfer was used as a source space for subsequent weighted minimum norm estimation. Source localization was performed thanks to the toolbox Brainstorm (version v. 3.191209 (09-Dec-2019) on Matlab R2012b) (Tadel et al., 2011).

A noise covariance matrix was computed on the resting state session of the experiment. The forward model was computed with the OpenMEEG software (OpenMEEG Software, <https://openmeeg.github.io/>, Gramfort et al., 2010). After coregistration between the individual anatomy and MEG sensors, cortical currents were estimated using a distributed model consisting of 15,002 currents dipoles from the time series of the 275 gradiometer signals, using a linear inverse estimator (weighted minimum-norm current estimate, signal-t-noise ratio of 3, whitening PCA, depth weighting of 0.5). Sources orientations were normality constrained to the orthogonality to the grey white matter boundary of the individual MRIs. The results were then projected on a standard brain model anatomy (ICBM152; 15,002 vertices) for group averaging purposes.

ERF sources analysis – Transient evoked responses (Band-Pass 2 to 30 Hz)

First, we computed the sources of the averaged 2nd, 3rd and 4th tones of the S1 and the DIS presented on the Left or Right side, separately, from -50 to +250ms (relative to the onset of the sound). To define regions of interest (ROIs) at the source level, we used t-test to zero to spot the emergence of the N1 component in these computed sources. We defined 6 regions of interest, 3 on each hemisphere contralateral to the sound presentation. The number of vertices in each ROI is reported in Table 3, and their localization is presented in Figure 32.

	Left Hemisphere	Right Hemisphere
Temporal	43	40
Inferior Frontal	16	21
Supra-Temporal Gyrus	28	33

Table 3 – Number of vertices in each region of interest of BP2-30 analysis.

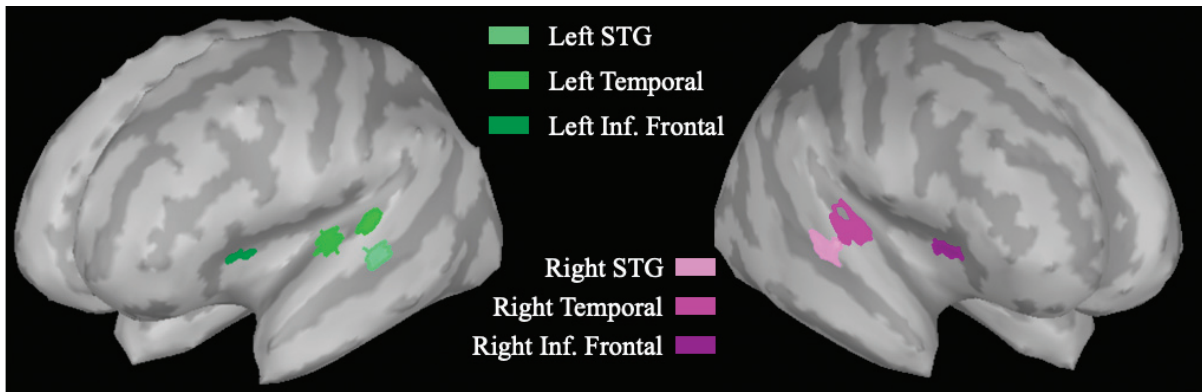


Figure 32 - Illustration of the regions of interest for the transient evoked response analysis. STG = Superior Temporal Gyrus; Inf. = Inferior

Effects of the conditions on peak amplitude were evaluated on extracted ROI time series. The recorded amplitude was averaged on a ± 25 ms time-window centered on maxima of the N1 peak, respectively. We computed the difference of this averaged amplitude between S1 and DIS. These N1(S1)-N1(DIS) values were then submitted to Bayesian ANOVAs with factors MEMORYload and DISdiff, for each studied scout (6), collapsed side of presentation. As a post-hoc investigation, the effect of DISdiff on both N1(S1) and N1(DIS) was evaluated thanks to Bayesian t-tests, for each ROI.

ERF sources analysis – Sustained evoked responses (Low-Pass 2Hz)

First, we computed the sources of the sustained evoked responses from -1 second to +7 seconds (relative to the onset of the S1+DIS presentation). To define regions of interest (ROIs) at the source level, we used the sources of the sustained evoked response during S1, using t-test to zero. We defined 2 regions of interest, 1 on each hemisphere. The number of vertices in each ROI is reported in Table 4, and their localization is presented in Figure 33.

	Left Hemisphere	Right Hemisphere
Temporal	66	68

Table 4 - Number of vertices for each region of interest for the sustained evoked response analysis.

Effects of the conditions on amplitude were evaluated on extracted ROI time series. The recorded amplitude was averaged for the time window corresponding to the S1+DIS display period, from 700 to 2000ms. These values were then submitted to Bayesian ANOVAs with factors MEMORYload and DISdiff, for each studied ROI (6), side of presentation collapsed.

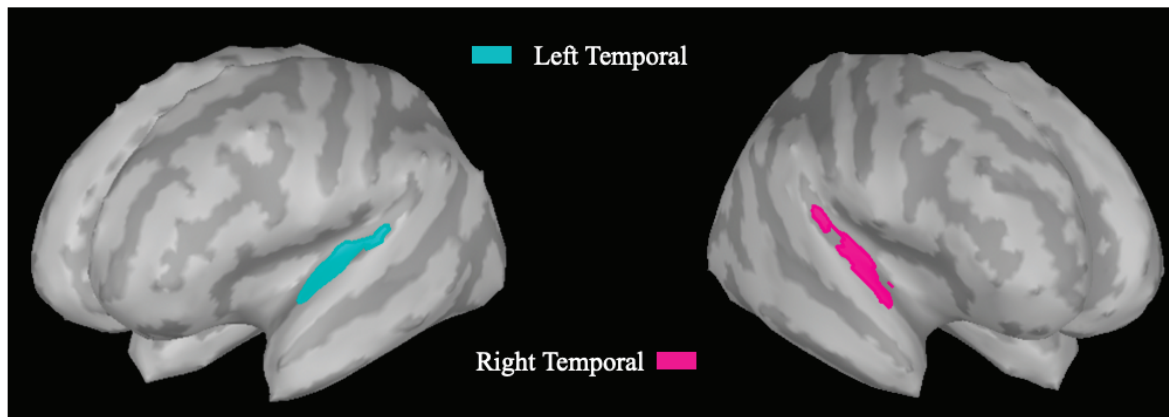


Figure 33 - Illustration of the LP2 regions of interest.

Oscillation sensor-level analysis

To investigate the dynamics of alpha power during the task, a time-frequency analysis of the different conditions was performed using the Fieldtrip toolbox (Oostenveld et al., 2011). Oscillatory power was computed from -2500 to +8000ms around the onset of the S1, using Morlet wavelet decomposition with a width of four cycles per wavelet ($m=7$; Tallon-Baudry & Bertrand, 1999), for frequencies from 5 to 20Hz, with steps of 1Hz, and using 50ms sliding windows. For each single trial, the corresponding ERF was subtracted before wavelet decomposition to focus on induced (and not evoked) activity.

Cluster-Based Permutation Tests were used to contrast the oscillatory power in different time windows of interest to the baseline period (-1800 to -1000 ms) mean power. Four time-windows were defined relative to S1 onset: (1) one during the cue presentation, before sounds onset, from -800 to 0ms, and three during the different events of a trial, i.e. (2) the presentation of S1 and DIS melodies, from 400 to 2000ms, (3) the retention gap, from 2400 to 4000ms, and (4) the presentation of S2 melody, from 4400 to 6000ms. The observations and statistics associated with oscillatory power allowed us to define the parameters of the source reconstruction.

Oscillation sources reconstruction

For source reconstruction of the alpha power, a grid with 0.5-cm resolution was normalized on a MNI template, and then morphed into the brain volume of each participant thanks to the Fieldtrip toolbox (Oostenveld et al., 2011). We used the frequency-domain adaptive spatial technique of dynamical imaging of coherent sources (DICS; Gross et al., 2001). Data from all conditions were concatenated, and the cross-spectral density (CSD) matrix (-2.5 to +7s, relative to S1 onset) was calculated using the multitaper method with a target frequency of 10 (+/-5) Hz. Leadfields for all grid points along with the CSD matrix were used to compute a common

spatial filter that was in turn used to estimate the spatial distribution of power for all time-frequency windows of interest. Afterward, power in each time window (-800:0ms; 400:1200ms; 1200:2000ms; 2400:3200ms; 3200:4000ms; 4400:5200ms; 5200:6000ms) was contrasted against a corresponding baseline pre-cue window (-1800:-1000ms) for frequencies 8 and 11Hz (+/- 1.25Hz) using a nonparametric cluster-based permutation analysis (Maris & Oostenveld, 2007). The time-frequency windows have been chosen according to the sensor-level results and previous findings dissociating low and high alpha modulations under auditory attention (ElShafei et al., 2018, 2020). For this test, cluster-based permutation tests control for multiple comparisons in the source space dimension.

Oscillation analysis on ROIs and virtual electrodes – preliminary investigations

The source-level analysis mentioned above provided a snapshot of the underlying cortical activity across conditions. In order to assess memory load and attentional filtering difficulty effects, we defined virtual electrodes within regions of interest (ROIs), in order to resolve the time-course activity at the source level. The ROIs are based on the Brodmann atlas: the *auditory ROI (Aud)* is composed of Brodmann areas 41, 42, and 22, the *visual ROI (Vis)* is composed of Brodmann areas 17, 18, and 19, the *frontal ROI* is composed of Brodmann areas 44, 45, and 46, and the *motor ROI* is composed of Brodmann areas 4 and 6. For each ROI, virtual electrodes were defined as the average of voxels included in these Brodmann areas.

In order to get a time-resolved estimation of source activity, we computed time-frequency at the level of virtual electrodes using the LCMV beamformer. Spatial filters were constructed from the covariance matrix of the averaged single trials at sensor level (-2.5:7s, relative to target onset, 1-20Hz, lambda 15%) and the respective leadfield by a linear constrained minimum variance (LCMV) beamformer (Van Veen et al., 1997). Then, spatial filters were multiplied by the sensor level data, thus obtaining the time course activity of each voxel of interest. Activity was averaged for each hemisphere separately.

For each ROI, we subtracted the evoked potentials (the signal averaged across trials) from each trial. Time-frequency power was then computed in the same manner as in the sensor level analysis, using Morlet wavelet decomposition.

Alpha power was averaged across time, between -0.8 and 6s for each ROI, to extract the power spectrum in each subject. Individual alpha peak frequency (APF) was defined separately for each ROI in each subject. For auditory and frontal virtual electrodes, the peak was defined as the frequency with the maximum alpha power decrease relative to baseline (-1.8 to -1s pre-target onset) between 5 and 15 Hz. For visual and motor ROIs, the peak was defined as the

frequency with the maximum alpha power increase relative to the baseline. The median APFs across subjects and hemispheres were 10 and 11Hz, 9 and 9Hz, 9 and 9Hz, 10 and 10Hz in the auditory, visual, frontal, and motor regions of interest in the left and right hemisphere respectively.

Alpha power was averaged across time from 400 to 2000ms and across frequencies from -1 to +1 Hz around the median APFs of each ROI. These average values were submitted to a Bayesian ANOVA with factors MEMORYload and DISdiff, for each ROI.

Results

Behavioral results

For d' (Figure 34-A., Sup.Table 51), the best model explaining the results of MEMAT is the one with factors MEMORYload, DISdiff and the interaction between MEMORYload and DISdiff ($BF_{10}=8.0e+22$). There is decisive evidence for MEMORYload ($BF_{inclusion}=1.4e+20$) and for DISdiff ($BF_{inclusion}=2.6e+7$) effects, and positive evidence for the MEMORYload x DISdiff interaction ($BF_{inclusion}=9.7$) (see Sup.Table 45 - Analysis of effects for the Bayesian ANOVA on d' (factors: GROUP, MEMORYload, DISdiff).

). d' are higher for easy-to-ignore distractors (easy DIS) compared to hard-to-ignore distracting melodies (hard DIS), and higher under low load compared to high memory load. Difference between hard DIS and easy DIS is less important when load is high compared to low. Post-hoc tests reveal decisive evidence for a difference between easy and hardDIS conditions under low memory load ($BF_{10}=18462.4$) and strong evidence for a difference between easy and hard DIS conditions under high memory load ($BF_{10}=56.5$).

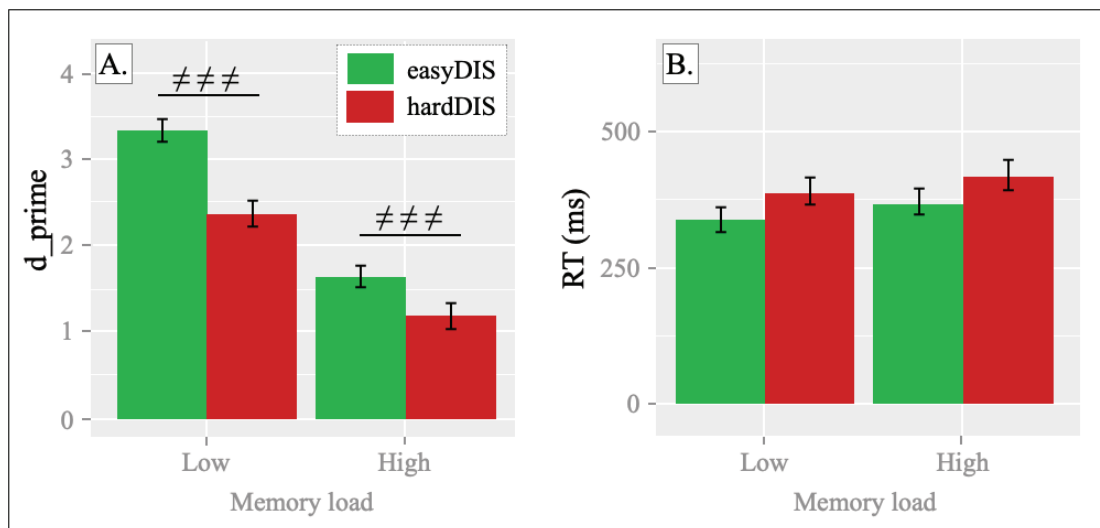


Figure 34 - Behavioral Results. Effects of the distraction difficulty and task load on d' -primes (A.) and RTs (B.). Results of post-hoc t -tests of the MEMORYload by DISdiff interaction on d' : "###" corresponds to $BF > 100$ (decisive evidence).

For the criterion, in agreement with previous studies using delayed-matching-to-sample tests, there is weak to strong evidence for positive c values (see Sup.Table 53), underlining that participants tended to miss differences between melodies. The best model explaining criterion results is the one with factors MEMORYload, DISdiff, and the interaction between MEMORYload and DISdiff ($BF_{10}=2.1e+12$) (see Sup.Table 54). There is decisive evidence for MEMORYload ($BF_{inclusion}=3.6e+10$) and for DISdiff ($BF_{inclusion}=2969.7$) effects, and weak evidence for the MEMORYload x DISdiff interaction ($BF_{inclusion}=2.4$) (see Sup.Table 55). Criterion is higher under high than low memory load and is higher for easy than hard distracting condition.

For the RTs (Figure 34-B.), the best model explaining results is the one with MEMORYload and DISdiff ($BF_{10}=5.9e+4$; see Sup.Table 56). There is strong evidence for DISdiff ($BF_{inclusion}=15.0$) and MEMORYload ($BF_{inclusion}=10.3$) effects (see Sup.Table 57).

RTs are longer for hard DIS compared to easy DIS, they are longer for high compared to low memory load.

These behavioral results replicate what we obtained in the previous behavioral experiment (see Article 1, SHARED COGNITIVE RESOURCES BETWEEN MEMORY AND ATTENTION DURING SOUND SEQUENCE ENCODING). In the following sections, we focused on the neural correlates associated with the observed effects of the difficulty of the distractors and the working memory load.

ERF results

Transient response analysis (BP2-30)

On the sensors, we can observe the presence of a P50, a N1 for each sound of S1 and DIS melodies (see Figure 35-A.). At the end of each sound, there is also a late positive deflection, just before the presentation of the following sound.

The N1 has been shown to be very sensitive to sound repetition: we can observe a latency increase and an amplitude decrease of the N1 response from one tone to the next one. In the following, we focused on the N1 response of the averaged signal for the 2nd, 3rd and 4th tones of the DIS and the S1 melodies separately (see Figure 35-B. and Figure 35-C.).

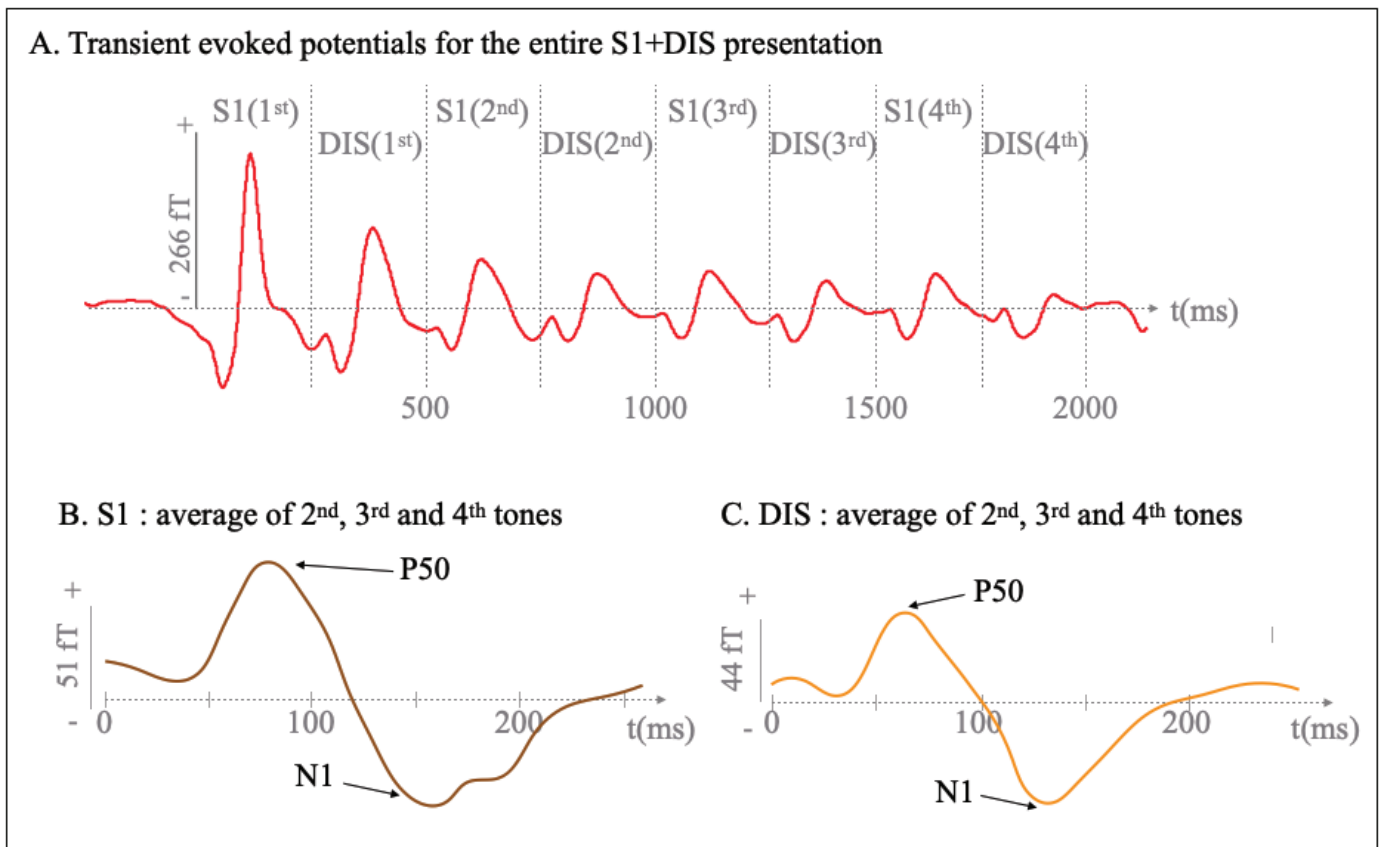


Figure 35 - Transient evoked potentials on a left temporal sensor (MLT15) averaged across participants, collapsed for all conditions, left and right presentation sides collapsed. A. Time window: from -250 to 2100ms, with the entire S1+DIS presentation. **B.** Averaged signal for the 2nd, 3rd, and 4th tones of S1 melody. **C.** Averaged signal for the 2nd, 3rd, and 4th tones of DIS melody.

Regarding the sources, we observe a P50 a N1, and a late positive deflection in each region of interest (see Figure 36).

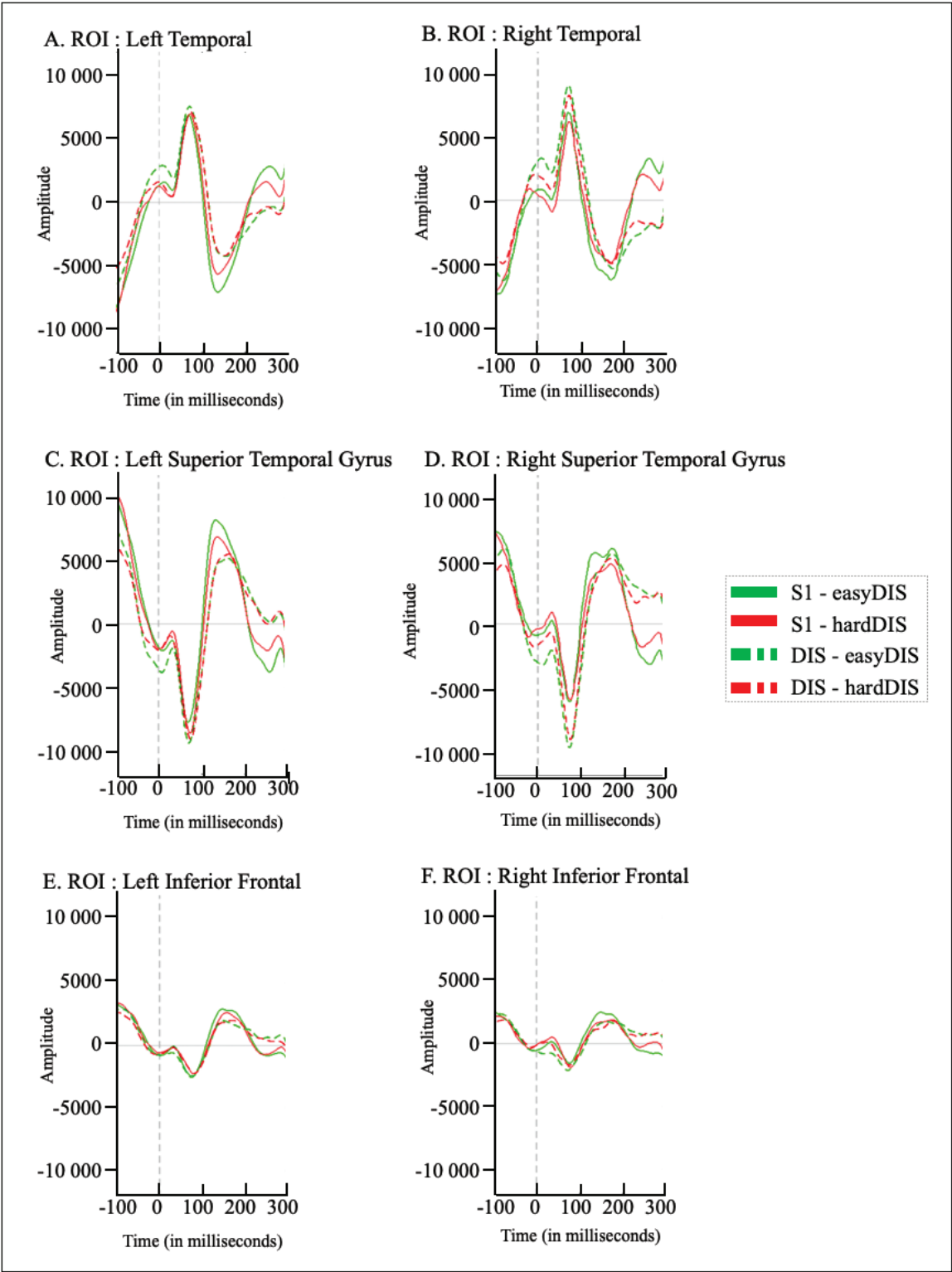


Figure 36 - Time-course of the evoked potentials for the different scouts, sorted by identity of the sound (S1 or DIS) and DISdiff (easy or hard), for all ROIs used in the analysis of transient evoked responses.

In the ANOVA for transient evoked responses with DISdiff and MEMORYload as factors, the best model explaining results for the difference N1(S1)-N1(DIS) is the one with the factor DISdiff, regardless of the region of interest (see Sup. Table 58 to Sup. Table 65). The difference between N1(S1) and N1(DIS) is greater in the easyDIS condition than in the hardDIS condition (see Figure 37).

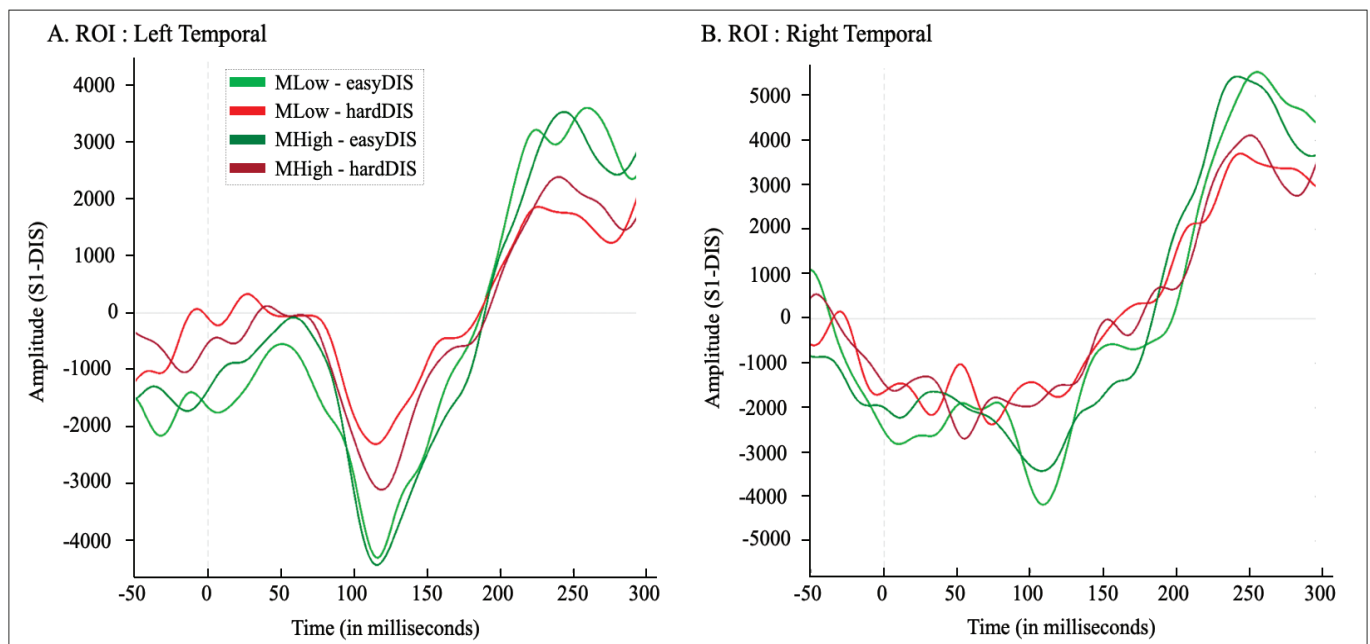


Figure 37 - Time course of the difference of recorded activity S1 minus DIS. Left (A.) and Right (B.) in temporal regions of interest, depending on the combination of the main conditions, MEMORYload (2 levels: MLow, MHigh) and DISdiff (2 levels: easyDIS, hardDIS).

Post-hoc tests reveal positive to strong evidence towards an effect of DISdiff on N1 to S1 tones and positive evidence for no effect of DISdiff on N1 to DIS tones, regardless of the region of interest (see Table 5). The N1 to S1 tones is greater in amplitude under the easyDIS condition than under the hardDIS condition (see Figure 36).

	N1(S1)		N1(DIS)	
	Left Hemisphere	Right Hemisphere	Left Hemisphere	Right Hemisphere
Temporal	87.6	19.2	0.2	0.2
Inferior Frontal	5.6	6.7	0.3	0.4
Supra-Temporal Gyrus	42.1	3.3	0.3	0.2

Table 5 - BF_{10} corresponding to the post-hoc t-tests easyDIS vs hardDIS for S1 and DIS separately, for each region of interest.

Sustained responses analysis (LP2)

We observe a deflection of the sustained evoked responses during the S1+DIS and S2 presentation periods of the trial. These plateau-shaped deflections are impacted at a smaller amplitude level by the presentation of each tone (see Figure 38).

In the following, we focus on the sustained evoked responses during the S1+DIS time window. In the ANOVA on the averaged sustained evoked responses amplitude across the S1+DIS time window, with DISdiff and MEMORYload as factors, the best model explaining the results is the one with the factor DISdiff (Left Temporal ROI: $BF_{10} = 399.4$; Right Temporal ROI: $BF_{10} = 1.7$) (see Sup. Table 70 to Sup. Table 73). The amplitude of the sustained response is larger for hard- compared to easy-to ignore distractors (see Figure 38).

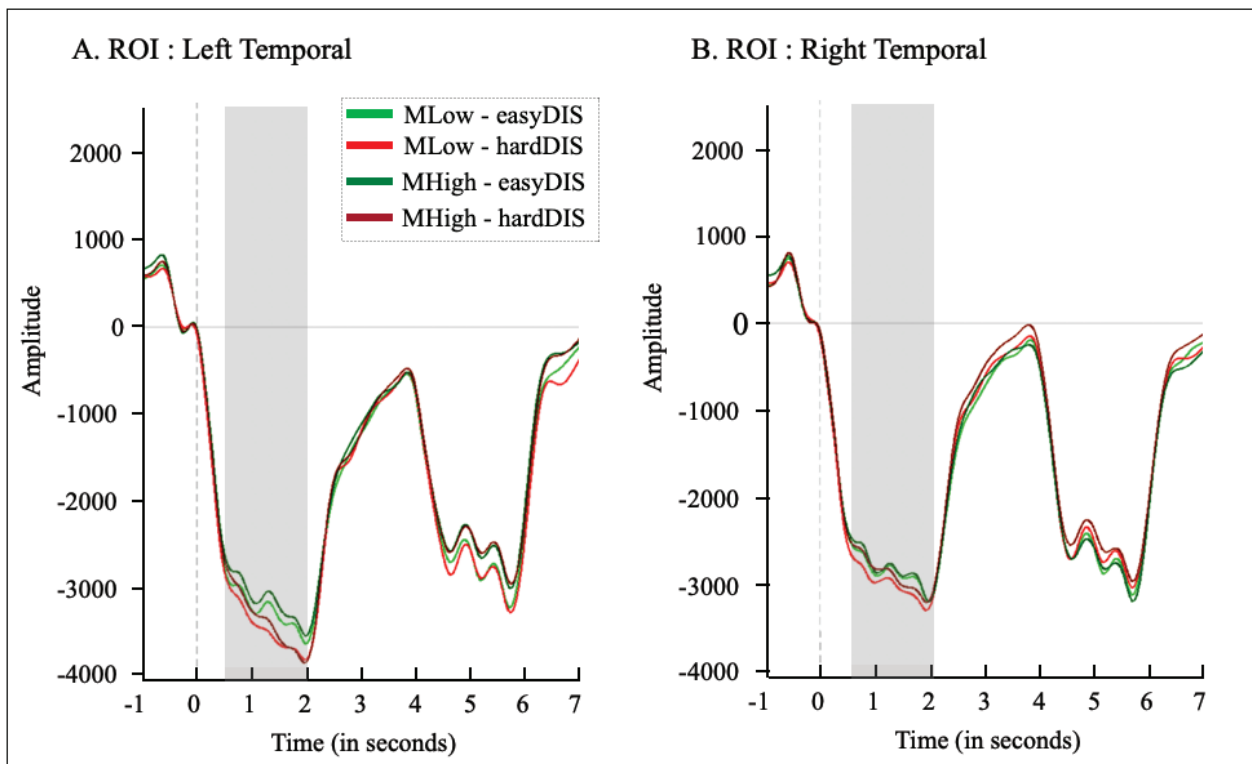


Figure 38 - Time course of the sustained evoked responses for Left and Right Temporal ROIs, sorted by main conditions MEMORYload (2 levels: MLow, MHigh) and DISdiff (2 levels: easyDIS, hardDIS). The window in grey indicates the time window of interest used for the analysis (700:2000ms).

Overall, the ERF analyses reveal a greater sustained response and a lower amplitude of the N1 to S1 tones when the distractors are harder to ignore.

Oscillations results

Results from sensor-level analysis

The time-frequency power charts computed on sensors (see Figure 39), with a baseline from -1.8 to -1s relative to S1+DIS onset reveal two profiles centered on two distinct frequencies: 8 and 11 Hz, called low- and high-alpha in the following. In the low alpha band, we can observe a decrease of power, also named a desynchronization, during the presentation of the S1 and DIS melodies. This low-alpha activity is observed at temporal sensors, especially in the left hemisphere (see Figure 39-A.). In parallel, in the high-alpha band, there is a decrease during the cue presentation, followed during the S1 and DIS presentation by an increase of power, also named a synchronization which lasts the entire trial. This high-alpha band is observed at occipital sensors (see Figure 39-B.).

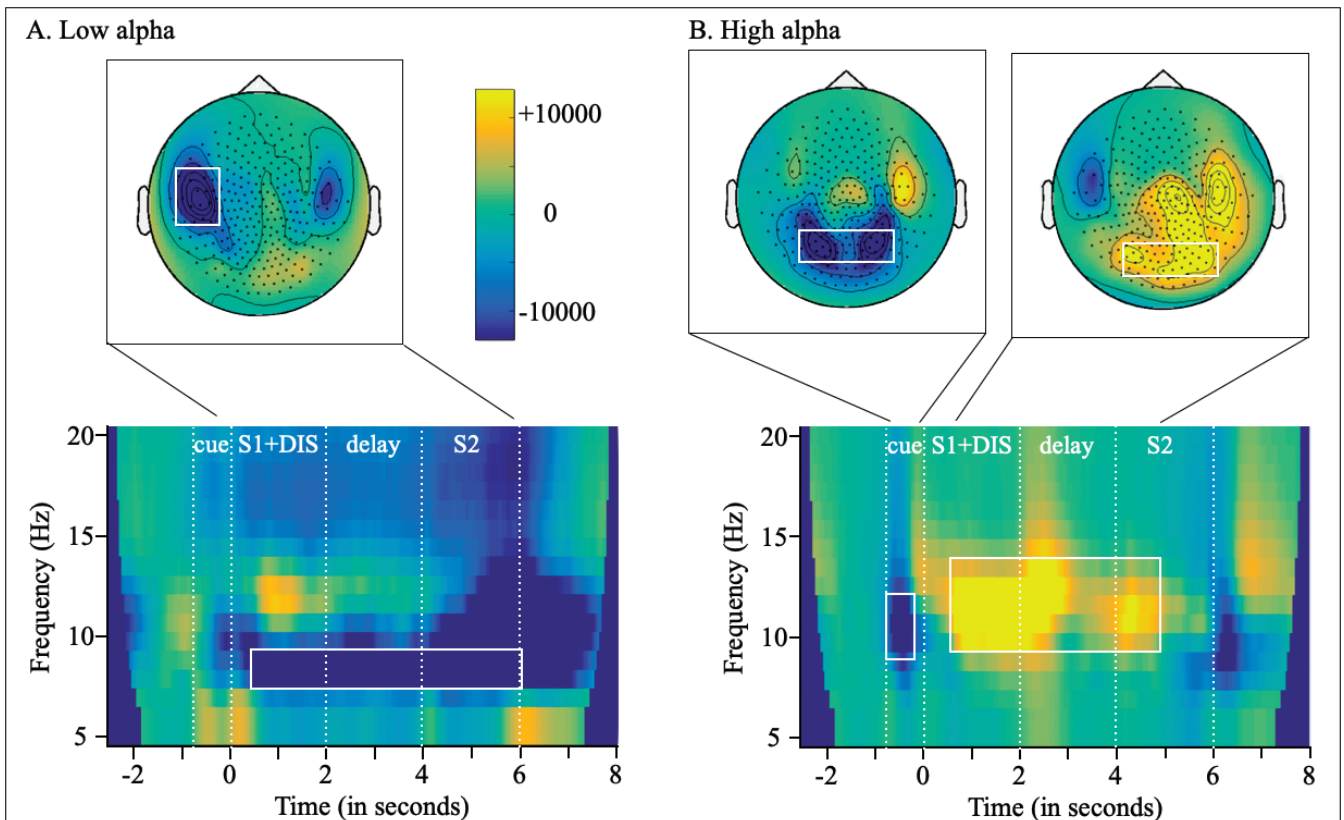


Figure 39 – Low (7-9Hz, A.) and high (10-12Hz, B.) alpha activity. First row: topographical maps of baseline corrected alpha power averaged in the two frequency bands during different latency windows. Baseline is -1800 to -1000ms relative to S1+DIS onset. A. time window: 0.4 to 6 seconds. B. time windows: -800 to 0ms (cue presentation), 0.4 to 5s. Second row: time-frequency representations of baseline-corrected alpha power averaged across sensors highlighted by the white boxes over the topographical maps on the first row.

Cluster-Based Permutation tests reveal significant (corrected $p < 0.05$) decrease of power during cue presentation and significant increase of power from 0 to 6 seconds in the occipital area for high alpha. For low alpha in the left temporal area, significance is reached from 4.4 to 6 seconds. During the S1+DIS presentation, p-value for 7-9Hz over the left temporal area is $p = 0.23$.

Visual inspection of the sensor data suggests a larger alpha synchronization on occipital sensors during the S1+DIS presentation for easyDIS in high compared to low memory load in the easyDIS condition, and in low compared to high memory load in the hardDIS condition. The occipital alpha desynchronization present during the cue seems greater for high compared to low memory load (see Figure 40).

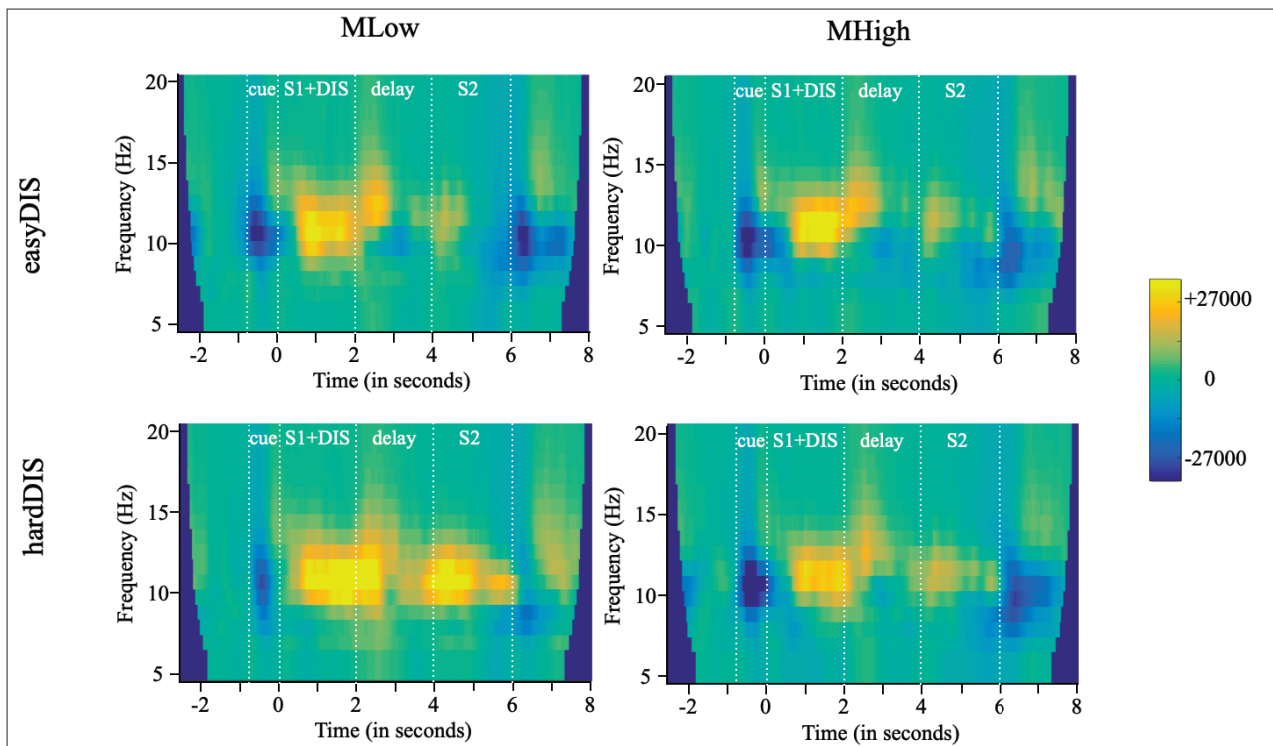


Figure 40 - Comparison of alpha oscillation power between conditions at the sensor level, for occipital sensors. Occipital sensors: MLO12,13,14,22,23,24,32,33,34,44, MRO12,13,14,22,23,24,32,33,34. Baseline applied: -1.8 to -1s relative to S1+DIS presentation.

The temporal alpha desynchronization during the S1+DIS presentation seems to be greater for high compared to low memory load, this difference being more important with easy than hard distractors (see Figure 41).

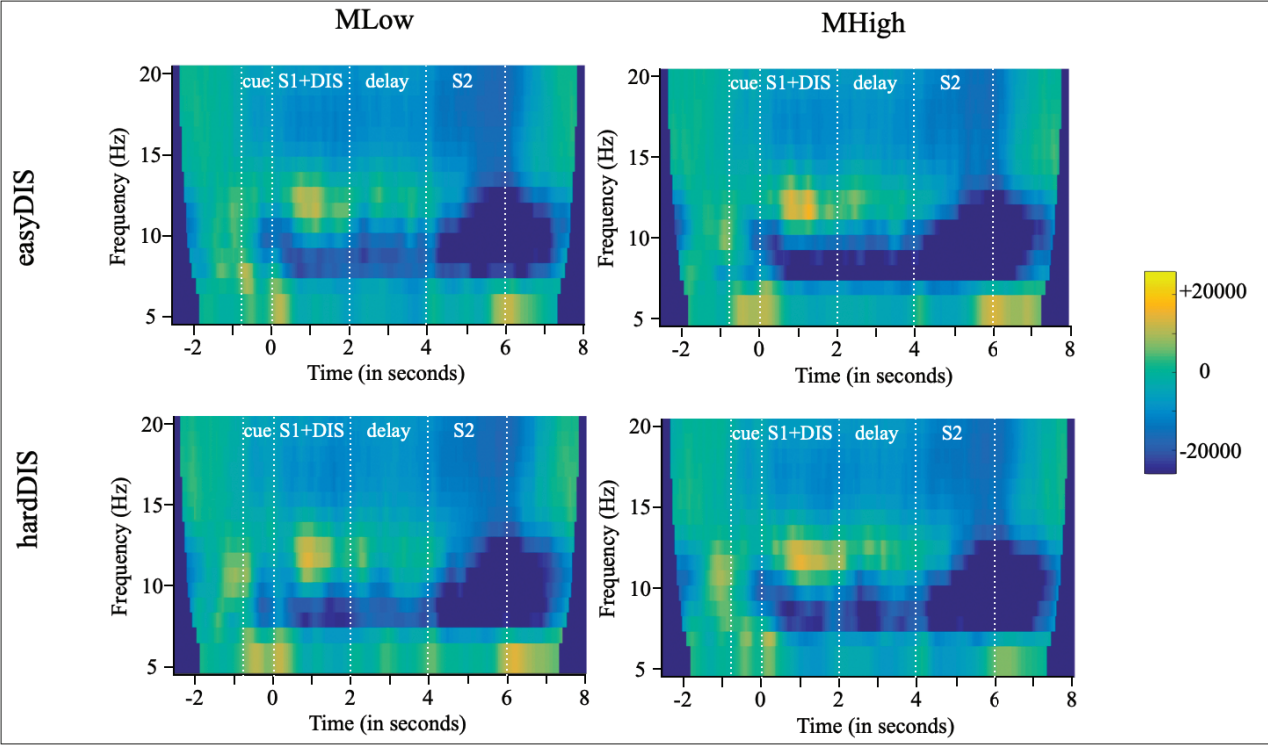


Figure 41 - Comparison of alpha oscillation power between conditions at the sensor level, for left temporal sensors. Occipital sensors: MLT11,12,13,14,22,23,24,32,33,34,41,42,43. Baseline applied: -1.8 to -1s relative to S1+DIS presentation.

Results from source analysis

Sources of these activities were computed and contrasted to the baseline window (-1800 to -1000ms relative to the onset of S1+DIS). A decrease in low alpha was observed in bilateral temporal and inferior frontal regions from -800ms to 6000ms (see topography in Figure 42-A. and Table 6). An increase in high alpha was observed in bilateral occipital and motor regions from 0 to 2500ms (see topography in Figure 42-A. and Table 6).

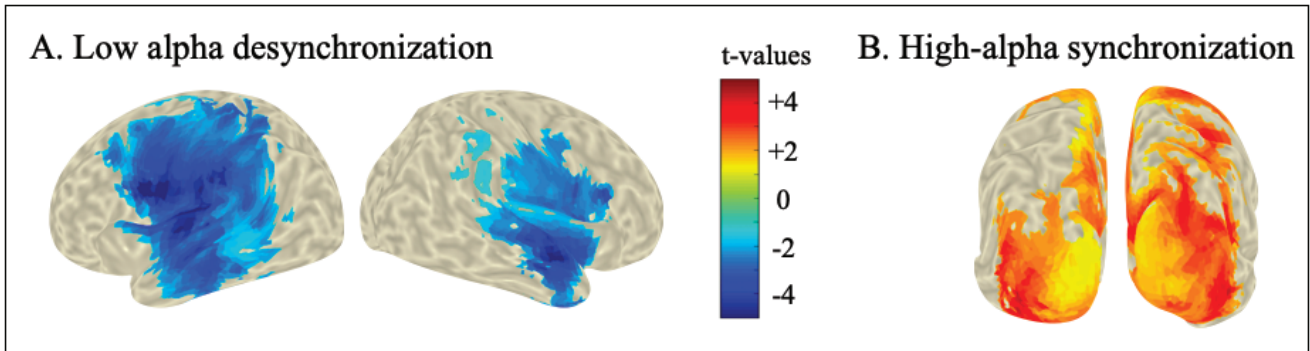


Figure 42 - Representation of the significant clusters during task performance, resulting from the cluster-based permutation tests, here illustrated in the case of the comparison of the 400 to 1200ms window to the baseline window (-1800 to -1000ms, relative to S1+DIS onset) for 6.75 to 9.25Hz (A.) and 9.75 to 12.25Hz (B.).

Time windows	-800 : 0	400 : 1200	1200 : 2000	2400 : 3200	3200 : 4000	4400 : 5200	5200 : 6000
6.75 to 9.25 Hz							
Left temporal cluster	0.01	0.002	0.01	0.02	0.05	0.02	0.02
Right temporal cluster	0.01	0.01	0.04	0.03	0.04	0.02	0.01
9.75 to 12.25 Hz							
Left occipital cluster	0.17	0.004	0.01	0.001	0.01	0.01	0.09
Right occipital cluster	0.41	0.001	0.001	0.001	0.003	0.003	0.05
9.75 to 12.25 Hz							
Left occipital cluster	0.01	0.06	0.04	0.13	0.09	0.02	0.001
Right occipital cluster	0.001	0.05	0.08	0.17	0.13	0.02	0.002

Table 6 – Results (corrected p-values) from cluster-based permutation tests to baseline for sources, on different time and frequency windows. Clusters presenting an increase or decrease in alpha power compared to baseline are highlighted in yellow or blue, respectively. Significant effects are highlighted in bold.

Results from ROI analysis – preliminary results

At the level of the virtual electrodes, we were able to confirm that the peaks of activity in the alpha oscillatory band are located at different frequencies depending on the ROI. Indeed, the median alpha frequency peak across subjects was 9 and 9 Hz for the Left and Right auditory ROIs, and 10 and 11 Hz for the Left and Right visual ROIs. The median alpha peak frequency across subjects was 9 and 9 Hz for the Left and Right Frontal ROIs, and 10 and 10 for the Left and Right Motor ROIs (see Figure 43).

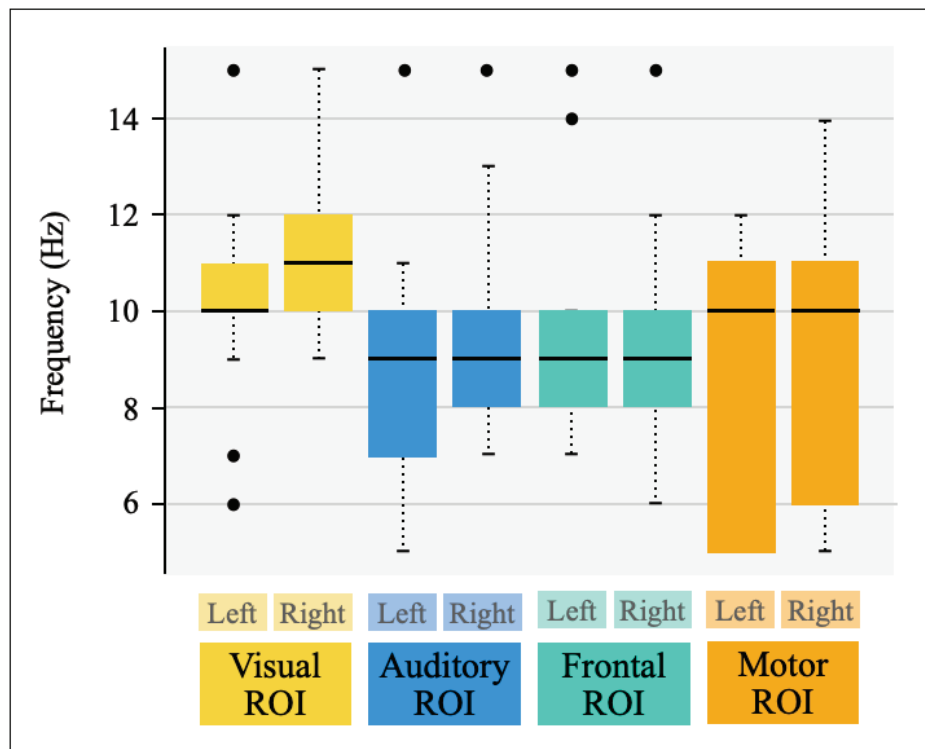


Figure 43 – Boxplot of individual alpha peak frequency in visual, auditory, frontal, and motor regions.

When performing an ANOVA with factors DISdiff and MEMORYload on the averaged alpha power around the median APF, it appears that for every ROI the best model explaining the averaged alpha frequency and S1+DIS window (400:2000ms) is the null model ($BF_{10}=1.0$, see Sup.Table 74 to Sup.Table 81).

With a closer look on the tendencies of averaged alpha power for each region of interest, it seems that there is no clear difference between low and high memory loads in the left visual and auditory ROIs (see Figure 44-A. and C.). This might be related to a larger amount of outliers for the APF in left visual ROI (see Figure 43), and a wide distribution of the APFs across participants for the left auditory ROI (see Figure 43). In the right visual ROI, the alpha

synchronization is higher for a high compared to a low memory load (see Figure 44-B.). There is a greater alpha desynchronization for a high compared to a low memory load in the right auditory ROI (see Figure 44-D.).

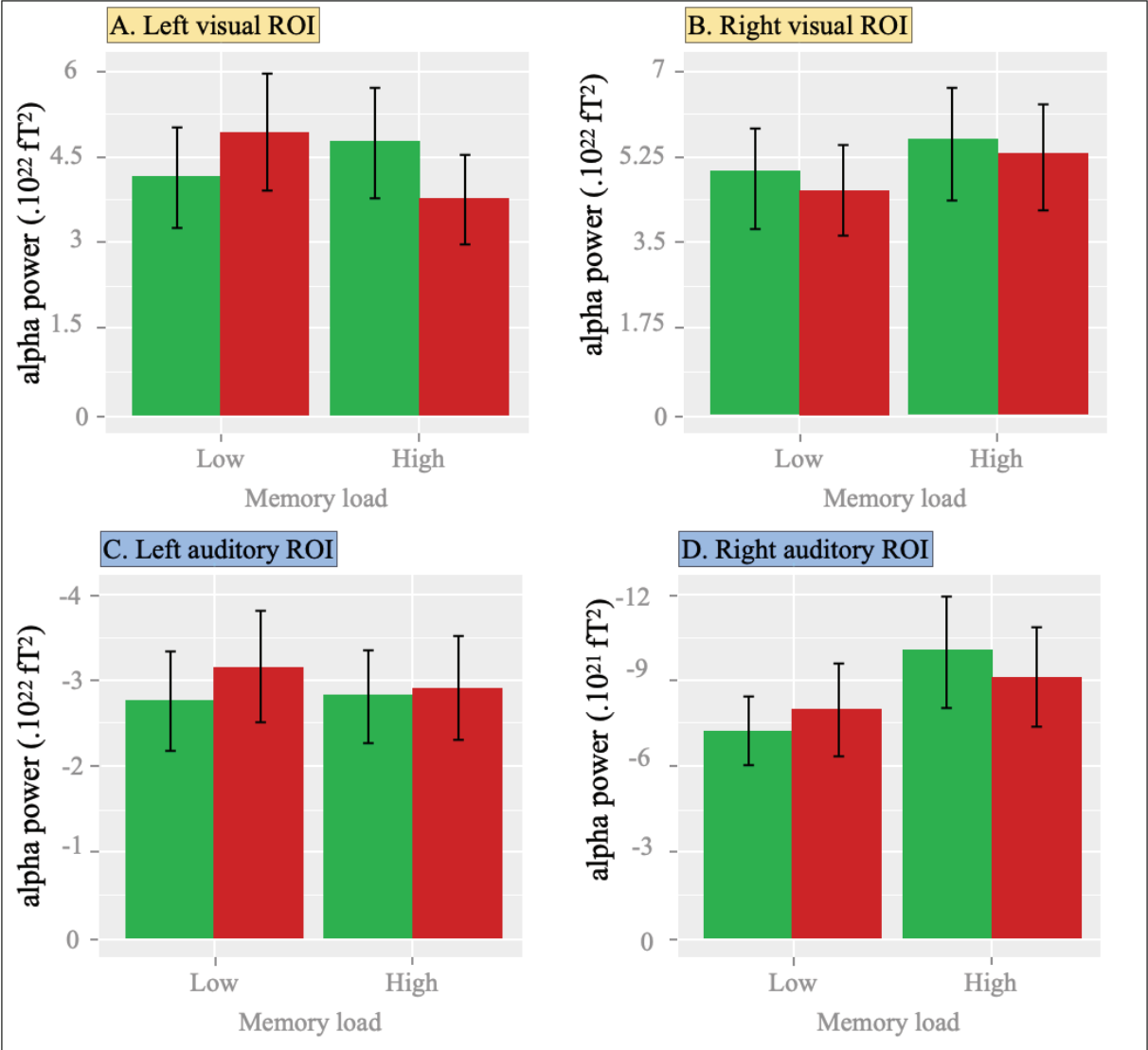


Figure 44 - Extracted alpha power around the median alpha frequency peak for the left and right visual and auditory regions of interest, during the S1+DIS presentation, according to the conditions DISdiff (two levels: easy, hard) and MEMORYload (two levels : MLow, MHigh. Alpha frequency peaks are respectively 10Hz, 11Hz, 9Hz and 9Hz (+/-1Hz) for the Left Visual, Right Visual, Left Auditory and Right Auditory regions of interest.

The tendencies of averaged alpha power in the left and right frontal ROIs are not coherent one to another, which can be due to the distribution of the APF across participants. Overall, the differences between the conditions are quite small (see Figure 45). There also appear to be no clear difference of averaged alpha power between the conditions for the left and right motor ROIs (see Figure 45).

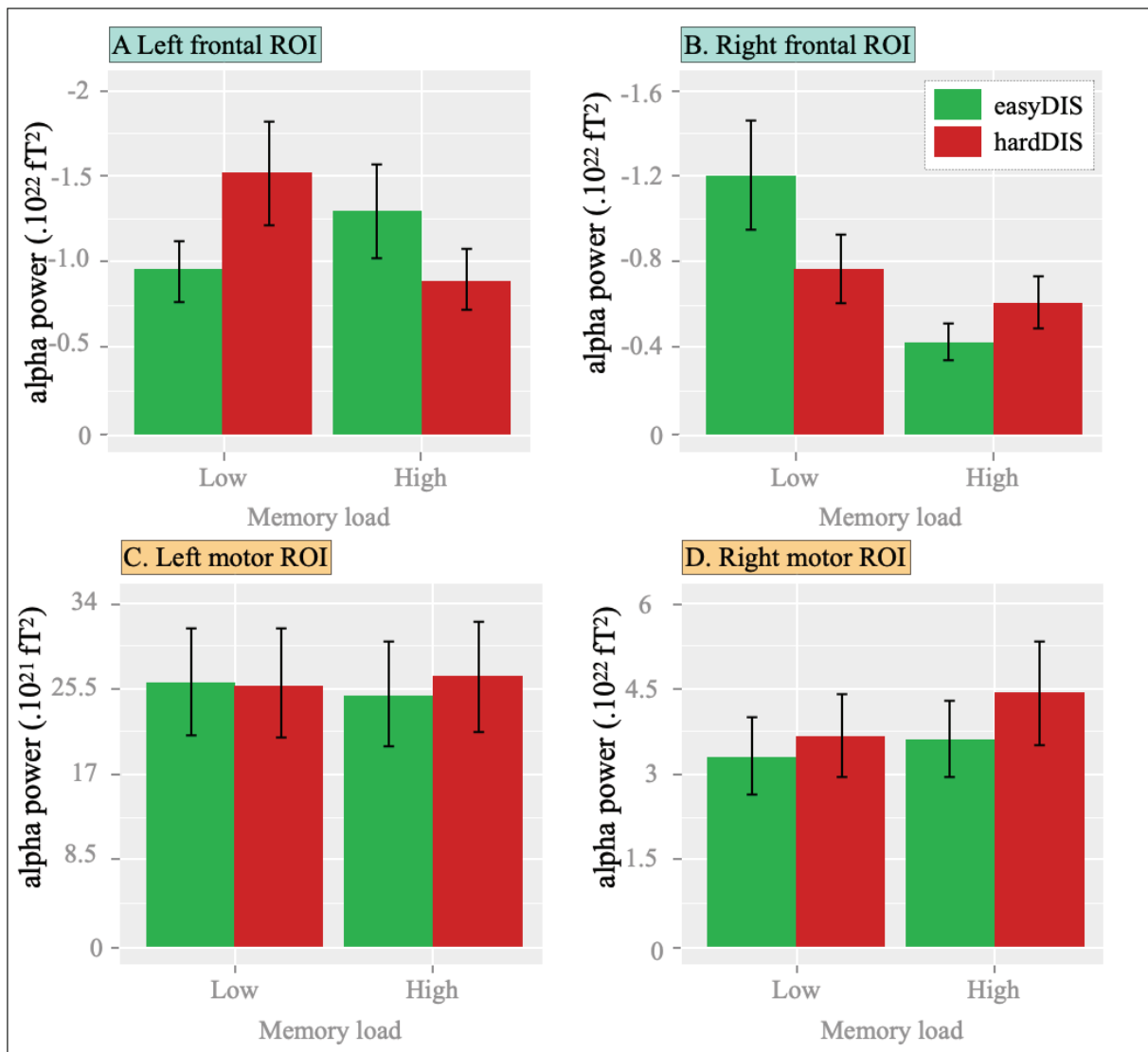


Figure 45 - Extracted alpha power around the median alpha frequency peak for the left and right frontal and motor regions of interest, during the S1+DIS presentation, according to the conditions DISdiff (two levels: easy, hard) and MEMORYload (two levels: MLow, MHigh). Alpha frequency peaks are respectively 9Hz, 9Hz, 10Hz and 10Hz (+/-1Hz) for the Left Frontal, Right Frontal, Left Motor and Right Motor regions of interest.

Discussion

Behavior

MEMAT paradigm allowed us to manipulate working memory and selective attention in an independent way. We found better performance in the presence of easy-to-ignore compared to hard-to-ignore distractors, a difference which is greater under low memory load. These behavioral results replicate in a different group of subjects, with a larger number of trials, the results first obtained with MEMAT (see Article 1, SHARED COGNITIVE RESOURCES BETWEEN MEMORY AND ATTENTION DURING SOUND SEQUENCE ENCODING).

ERFs

We found that the difference between S1 and DIS is modulated by the difficulty of the distractors, the amplitude of the N1 for S1 being reduced when associated distractors are hard- compared to easy-to-ignore. As there is an absence of effect of the distractors difficulty on N1(DIS), this effect cannot be due to refractoriness or perceptual load effects. These results suggest that so many resources are recruited to inhibit hard-to-ignore distractors recruit so many resources that there are not numerous enough to facilitate S1 processing. Very few studies have compared several levels of distractors difficulty in a dichotic listening task, but in a study from Alain and colleagues, for example, it appears that it was the inhibition of the distractors, rather than the facilitation of the targets, that was impacted by different distracting levels (Alain et al., 1993). This can be due to the associated working memory task, which puts more pressure on the encoding of the S1 than on the filtering of the distractors.

Sustained responses are also impacted by the difficulty of the distractors, without evidence in favor of an impact of the memory load: the recorded amplitude is higher for hard- compared to easy-to-ignore distractor conditions. This could either reflect a greater perceptual encoding process for the targets, either a larger attentional process. This absence of significant difference between memory loads differs from previous results with a similar delay matching-to-sample working memory task using melody stimuli (Albouy et al., 2013). However, this other experiment was devoid of attention manipulation, and the difference between memory loads was higher. In MEMAT, there is a possibility for the selective attention task to recruit all the resources during the encoding period.

Overall, participants seem to make a greater effort when distractors are difficult to filter out (reflected in the sustained response). But despite this, the amplitude of the N1 for the target (which can be assumed to reflect the quality of the encoding in memory), does not reach the one reached when the distractors are easy to filter. This degraded level of processing of S1 during encoding might be sufficient when the memory task is easy, but not when the memory task is difficult. Surely one could in the future try to dig in this direction by looking at the correlations between the amplitude of N1 and behavioural performance, especially in the Mhigh/hardDIS condition.

Oscillations

We observed modulations of activity in two different alpha sub-bands, related to different brain areas: a low-alpha band (7 to 9 Hz) associated with a temporal (auditory) generator, and a high-alpha band (10 to 12Hz) located in the occipital area. This result is in line with previous results from ElShafei and collaborators, obtained with another attention task (ElShafei et al., 2018).

If there seems to be modulations of alpha oscillatory activities depending on memory loads, we found no significant difference between conditions in the regions of interest investigated here. However, these results are only partial and would need to be more deeply investigated. In particular, the use of the median alpha peak frequency might not be appropriate, as alpha peaks seem to be rather different from one participant to another. This natural variability of alpha might indicate the necessity to use frequency bands specific to each participant. Several outlier participants might also need to be removed from analysis.

If we focused our analyses on alpha oscillations in the auditory and visual areas, we also aimed at testing frontal and motor areas. Indeed, we observed alpha oscillations in the prefrontal cortex, and aim to look on its modulation by selective attention but also by working memory. The motor cortex is very close to the auditory cortex; therefore, studying its alpha pattern of activation would help us to confirm that what we observe in the auditory cortex is indeed a reflection of auditory processes, and not an extension of what happens in the motor cortex.

Interaction effects

In this first round of MEG analyses, we found no significant interaction between selective attention and working memory in any of the explored brain activities, contrarily to what was observed in the behavioral data. Here, we focused on the N1, sustained responses, and alpha oscillations occurring during the S1+DIS presentation. There is still room for deeper investigations including during the delay or S2 phases of the trial, for example, but gamma oscillations are also of interest, as presented in the general introduction of this thesis.

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Supplementary data

Behavioral data

ANOVA on d' with MEMORYload and DISdiff as factors

d'	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.200	1.1e-23	4.5e-23	1.0	
	MEMORYload	0.200	3.7e-9	1.5e-8	3.3e+14	1.9
	DISdiff	0.200	6.3e-22	2.5e-21	56.5	0.9
	MEMORYload + DISdiff	0.200	0.1	0.4	8.3e+21	3.0
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.200	0.9	38.7	8.1e+22	46.9

Sup. Table 51 - Bayesian ANOVA results for the analysis of d' (factors: MEMORYload, DISdiff).

d'	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.400	0.094	1.4e+20
	DISdiff	0.400	0.094	2.6e+7
	MEMORYload * DISdiff	0.200	0.094	9.7

Sup. Table 52 - Analysis of effects for the Bayesian ANOVA on d' (factors: MEMORYload, DISdiff).

Criterion data: BF₁₀ corresponds to the comparison to zero (Bayesian one-sample t-test)

		MEMAT - MEG		
		mean	SD	BF ₁₀
Low Memory	Easy DIS	0.2	0.3	3.5
	Hard DIS	0.0	0.3	0.2
High Memory	Easy DIS	0.7	0.4	334 862.6
	Hard DIS	0.4	0.3	16 895.5

Sup. Table 53 - Criterion data (mean, SD: standard deviation) for all conditions (2 levels of MEMORYload × 2 levels of DISdiff). BF10 correspond to Bayesian one-sample test comparison to zero.

ANOVA on criterion with MEMORYload and DISdiff as factors

c	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.200	3.4e-13	1.3e-12	1.0	
	MEMORYload	0.200	9.9e-5	3.9e-4	2.9e+8	1.5
	DISdiff	0.200	7.8e-12	3.1e-11	23.2	1.7
	MEMORYload + DISdiff	0.200	0.3	1.7	8.7e+11	1.4
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.200	0.7	9.7	2.1e+12	1.8

Sup. Table 54 - Bayesian ANOVA results for the analysis of c (factors: MEMORYload, DISdiff).

c	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.400	0.3	3.6e+10
	DISdiff	0.400	0.3	2969.7
	MEMORYload * DISdiff	0.200	0.7	2.4

Sup. Table 55 - Analysis of effects for the Bayesian ANOVA on c (factors: MEMORYload, DISdiff).

ANOVA on RTs with MEMORYload and DISdiff as factors

RT	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.200	1.2e-5	4.8e-5	1.0	
	MEMORYload	0.200	4.0e-5	1.6e-4	3.3	1.2
	DISdiff	0.200	0.1	0.3	5673.0	1.0
	MEMORYload + DISdiff	0.200	0.7	9.8	58589.1	1.9
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.200	0.2	1.1	18289.3	3.6

Sup. Table 56 - Bayesian ANOVA results for the analysis on RT (factors: MEMORYload, DISdiff).

RT	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.400	0.7	10.3
	DISdiff	0.400	0.8	14980.0
	MEMORYload * DISdiff	0.200	0.2	0.3

Sup. Table 57 - Analysis of effects for the Bayesian ANOVA on RT (factors: MEMORYload, DISdiff).

ANOVA on N1(S1)-N1(DIS) amplitude (-/+25ms around the peak) with MEMORYload and DISdiff as factors

Left Temporal BP2-30 ROI

N1(S1)-N1(DIS)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.0	0.0	1.000	
	DISdiff	0.2	0.5	4.6	146.0	0.9
	MEMORYload + DISdiff	0.2	0.3	2.1	95.0	1.8
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.1	0.5	30.9	2.8
	MEMORYload	0.2	0.0	0.0	0.5	1.0

Sup. Table 58 - Bayesian ANOVA results for the analysis on N1(S1)-N1(DIS) amplitude difference (factors: MEMORYload, DISdiff) for the Left Temporal BP2-30 Region of interest.

N1(S1)-N1(DIS)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.3	0.7
	DISdiff	0.4	0.9	156.7
	MEMORYload * DISdiff	0.2	0.1	0.3

Sup. Table 59 - Analysis of effects for the Bayesian ANOVA on N1(S1)-N1(DIS) amplitude difference (factors: MEMORYload, DISdiff) for the Left Temporal BP2-30 Region of interest.

Right Temporal BP2-30 ROI

N1(S1)-N1(DIS)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.1	0.2	1.0	
	DISdiff	0.2	0.7	10.0	12.6	1.2
	MEMORYload + DISdiff	0.2	0.2	0.8	3.0	3.8
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.0	0.2	0.8	3.0
	MEMORYload	0.2	0.0	0.1	0.2	1.0

Sup. Table 60 - Bayesian ANOVA results on N1(S1)-N1(DIS) (factors: MEMORYload, DISdiff) for the Left Temporal BP2-30 Region of interest.

N1(S1)-N1(DIS)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.2	0.2
	DISdiff	0.4	0.9	12.8
	MEMORYload * DISdiff	0.2	0.0	0.3

Sup. Table 61 - Analysis of effects for the Bayesian ANOVA on N1(S1)-N1(DIS) (factors: MEMORYload, DISdiff) for the Right Temporal BP2-30 Region of interest.

Left Superior Temporal Gyrus BP2-30 ROI

N1(S1)-N1(DIS)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.0	0.1	1.0	
	DISdiff	0.2	0.6	4.9	31.0	1.4
	MEMORYload + DISdiff	0.2	0.3	1.6	16.4	1.7
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.1	0.6	7.2	2.3
	MEMORYload	0.2	0.0	0.0	0.5	1.1

Sup. Table 62 - Bayesian ANOVA on N1(S1)-N1(DIS) (factors: MEMORYload, DISdiff) for the Left Superior Temporal Gyrus BP2-30 region of interest.

N1(S1)-N1(DIS)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.3	0.5
	DISdiff	0.4	0.8	32.2
	MEMORYload * DISdiff	0.2	0.1	0.4

Sup. Table 63 - Analysis of effects for the Bayesian ANOVA on N1(S1)-N1(DIS) (factors: MEMORYload, DISdiff) for the Left Superior Temporal Gyrus BP2-30 region of interest.

Right Superior Temporal Gyrus BP2-30 ROI

N1(S1)-N1(DIS)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.1	0.7	1.0	
	DISdiff	0.2	0.61	6.3	4.2	1.1
	MEMORYload + DISdiff	0.2	0.2	0.7	1.1	2.5
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.1	0.2	0.3	3.9
	MEMORYload	0.2	0.0	0.1	0.2	0.9

Sup. Table 64 - Bayesian ANOVA on N1(S1)-N1(DIS) (factors: MEMORYload, DISdiff) for the Right Superior Temporal Gyrus BP2-30 region of interest.

N1(S1)-N1(DIS)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.2	0.3
	DISdiff	0.4	0.8	4.2
	MEMORYload * DISdiff	0.2	0.1	0.3

Sup. Table 65 - Analysis of effects the Bayesian ANOVA on N1(S1)-N1(DIS) (factors: MEMORYload, DISdiff) for the Right Superior Temporal Gyrus BP2-30 region of interest.

Left Inferior Frontal BP2-30 ROI

NI(S1)-NI(DIS)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.1	0.3	1.0	
	DISdiff	0.2	0.4	3.0	5.9	1.5
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.2	1.3	3.3	2.1
	MEMORYload + DISdiff	0.2	0.2	1.1	3.0	1.9
	MEMORYload	0.2	0.0	0.1	0.5	1.4

Sup.Table 66 - Bayesian ANOVA results on NI(S1)-NI(DIS) (factors: MEMORYload, DISdiff) for the Left Inferior Frontal BP2-30 Region of interest.

NI(S1)-NI(DIS)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.3	0.5
	DISdiff	0.4	0.7	6.0
	MEMORYload * DISdiff	0.2	0.2	1.1

Sup.Table 67 - Analysis of effects for the Bayesian ANOVA on NI(S1)-NI(DIS) (factors: MEMORYload, DISdiff) for the Left Inferior Frontal BP2-30 Region of interest.

Right Inferior Frontal BP2-30 ROI

NI(S1)-NI(DIS)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.3	1.3	1.0	
	DISdiff	0.2	0.4	2.8	1.6	0.9
	MEMORYload + DISdiff	0.2	0.2	0.8	0.7	2.6
	MEMORYload	0.2	0.1	0.4	0.4	0.9
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.1	0.3	0.3	2.7

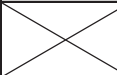
Sup.Table 68 - Bayesian ANOVA on NI(S1)-NI(DIS) (factors: MEMORYload, DISdiff) for the Right Inferior Frontal BP2-30 Region of interest.

NI(S1)-NI(DIS)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.3	0.4
	DISdiff	0.4	0.6	1.7
	MEMORYload * DISdiff	0.2	0.1	0.4

Sup.Table 69 - Analysis of effects for the Bayesian ANOVA on NI(S1)-NI(DIS) (factors: MEMORYload, DISdiff) for the Right Inferior Frontal BP2-30 Region of interest.

ANOVA on mean amplitude for the sustained evoked responses with MEMORYload and DISdiff as factors

Left Temporal LP2 ROI

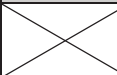
Averaged amplitude (700:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.0	0.0	1.0	
	DISdiff	0.2	0.5	4.3	399.4	1.0
	MEMORYload + DISdiff	0.2	0.4	2.3	282.6	1.6
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.1	0.5	86.5	2.4
	MEMORYload	0.2	0.0	0.0	0.5	1.1

Sup. Table 70 - Bayesian ANOVA results for the analysis on averaged amplitude (700:2000ms) of the sustained evoked response (factors: MEMORYload, DISdiff) for the Left Temporal ROI.

Averaged amplitude (700:2000ms)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.4	0.7
	DISdiff	0.4	0.9	440.5
	MEMORYload * DISdiff	0.2	0.1	0.3

Sup. Table 71 - Analysis of effects for the Bayesian ANOVA on averaged amplitude (700:2000ms) of the sustained evoked response (factors: MEMORYload, DISdiff) for the Left Temporal ROI.

Right Temporal LP2 ROI

Averaged amplitude (700:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.2	1.1	1.0	
	DISdiff	0.2	0.4	2.3	1.7	2.1
	MEMORYload + DISdiff	0.2	0.2	1.0	1.0	1.7
	MEMORYload	0.2	0.1	0.6	0.6	3.4
	MEMORYload + DISdiff + MEMORYload * DISdiff	0.2	0.1	0.4	0.4	3.9

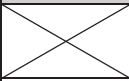
Sup. Table 72 - Bayesian ANOVA results for the analysis on averaged amplitude (700:2000ms) of the sustained evoked response (factors: MEMORYload, DISdiff) for the Right Temporal ROI.

Averaged amplitude (700:2000ms)	Effects	P(incl)	P(incl data)	BF _{Inclusion}
	MEMORYload	0.4	0.3	0.6
	DISdiff	0.4	0.6	1.7
	MEMORYload * DISdiff	0.2	0.1	0.4

Sup. Table 73 - Analysis of effects for the Bayesian ANOVA on averaged amplitude (700:2000ms) of the sustained evoked response (factors: MEMORYload, DISdiff) for the Right Temporal ROI.


ANOVA on mean alpha power with MEMORYload and DISdiff as factors

Left Visual alpha ROI

Averaged alpha power (9:11Hz, 400:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.640	7.102	1.000	
	MEMORYload	0.2	0.159	0.755	0.248	0.757
	DISdiff	0.2	0.139	0.644	0.217	0.752
	MEMORYload + DISdiff	0.2	0.039	0.161	0.060	6.375
	MEMORYload + DISdiff +MEMORYload * DISdiff	0.2	0.024	0.099	0.038	1.953


Sup.Table 74 - Bayesian ANOVA results for the analysis of averaged alpha power (9:11Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Left Visual region of interest.

Right Visual alpha ROI

Averaged alpha power (10:12Hz, 400:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.613	6.337	1.000	
	MEMORYload	0.2	0.173	0.839	0.283	1.351
	DISdiff	0.2	0.144	0.671	0.234	1.222
	MEMORYload + DISdiff	0.2	0.047	0.198	0.077	12.998
	MEMORYload + + DISdiff +MEMORYload * DISdiff	0.2	0.023	0.093	0.037	40.212


Sup.Table 75 - Bayesian ANOVA results for the analysis of averaged alpha power (10:12Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Right Visual region of interest.

Left Auditory alpha ROI

Averaged alpha power (8:10Hz, 400:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.402	2.691	1.000	
	MEMORYload	0.2	0.391	2.566	0.972	0.804
	DISdiff	0.2	0.092	0.405	0.228	2.238
	MEMORYload + DISdiff	0.2	0.087	0.382	0.217	1.465
	MEMORYload + + DISdiff +MEMORYload * DISdiff	0.2	0.028	0.115	0.070	2.881


Sup.Table 76 - Bayesian ANOVA results for the analysis of averaged alpha power (8:10Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Left Auditory region of interest.

Right Auditory alpha ROI

Averaged alpha power (8:10Hz, 400:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.632	6.860	1.000	
	MEMORYload	0.2	0.159	0.757	0.252	1.993
	DISdiff	0.2	0.158	0.753	0.251	1.030
	MEMORYload + DISdiff	0.2	0.039	0.162	0.062	1.629
	MEMORYload ++ DISdiff +MEMORYload * DISdiff	0.2	0.012	0.048	0.019	3.323


Sup.Table 77 - Bayesian ANOVA results for the analysis of averaged alpha power (8:10Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Right Auditory region of interest.

Left Frontal alpha ROI

Averaged alpha power (8:10Hz, 400:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.486	3.779	1.000	
	MEMORYload	0.2	0.308	1.783	0.635	1.027
	DISdiff	0.2	0.115	0.517	0.236	1.779
	MEMORYload + DISdiff	0.2	0.070	0.302	0.144	1.314
	MEMORYload ++ DISdiff +MEMORYload * DISdiff	0.2	0.021	0.087	0.044	2.016

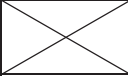
Sup.Table 78 - Bayesian ANOVA results for the analysis of averaged alpha power (8:10Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Left Frontal region of interest.

Right Frontal alpha ROI

Averaged alpha power (8:10Hz, 400:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.579	5.495	1.000	
	MEMORYload	0.2	0.214	1.092	0.370	2.538
	DISdiff	0.2	0.140	0.650	0.242	0.884
	MEMORYload + DISdiff	0.2	0.050	0.211	0.087	1.252
	MEMORYload ++ DISdiff +MEMORYload * DISdiff	0.2	0.017	0.069	0.029	4.146

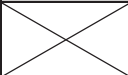
Sup.Table 79 - Bayesian ANOVA results for the analysis of averaged alpha power (8:10Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Right Frontal region of interest.

Left Motor alpha ROI

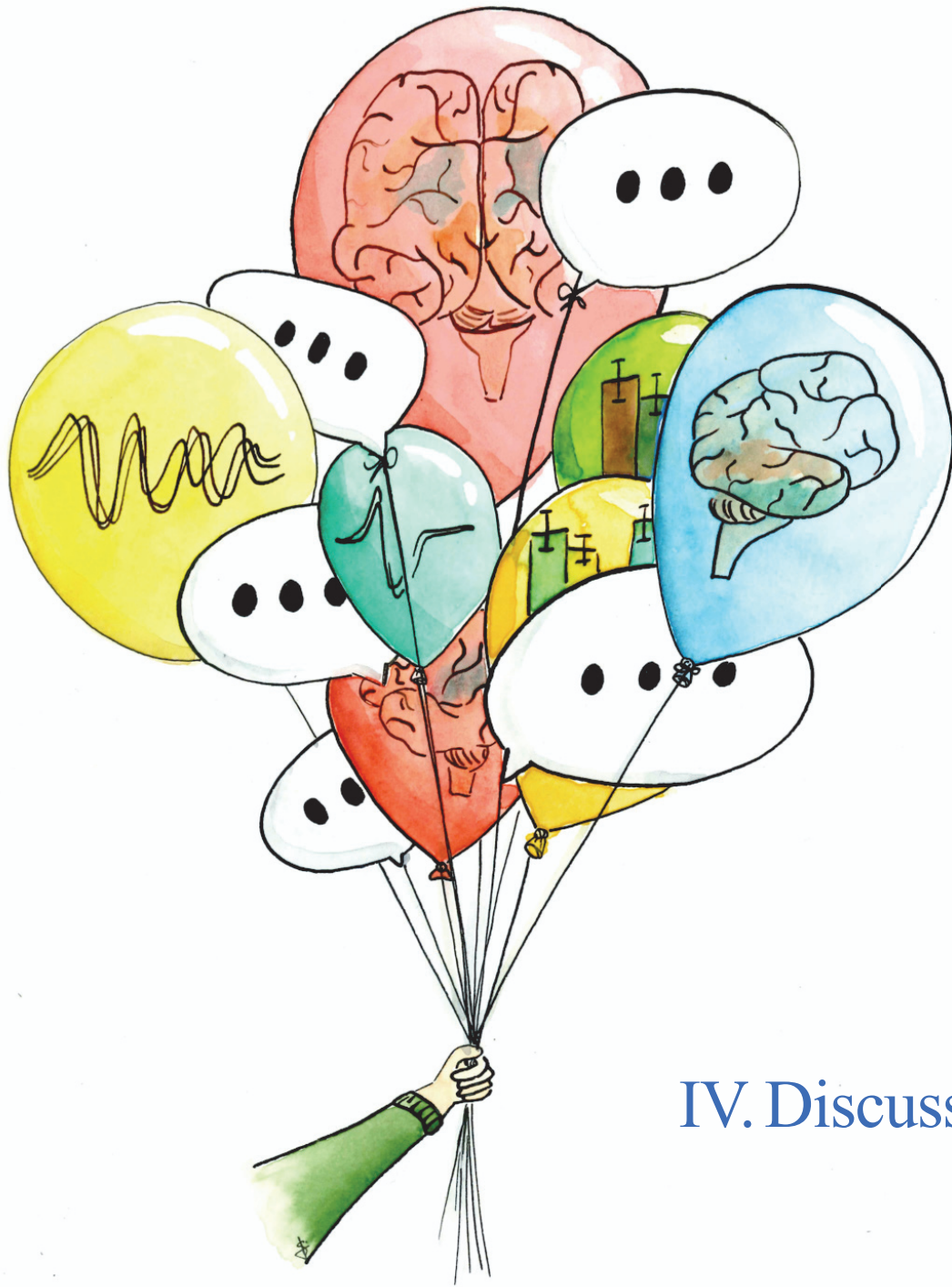
Averaged alpha power (9:11Hz, 400:2000ms)	Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.632	6.882	1.000	
	MEMORYload	0.2	0.166	0.795	0.262	0.990
	DISdiff	0.2	0.149	0.699	0.235	2.161
	MEMORYload + DISdiff	0.2	0.040	0.165	0.063	2.744
	MEMORYload ++ DISdiff +MEMORYload * DISdiff	0.2	0.013	0.054	0.021	8.945

Sup.Table 80 - Bayesian ANOVA results for the analysis of averaged alpha power (9:11Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Left Motor region of interest.

Right Motor alpha ROI

Averaged alpha power (9:11Hz, 400:2000ms)		P(M)	P(M data)	BF _M	BF ₁₀	error %
	Null model (incl. subject)	0.2	0.503	4.040	1.000	
	MEMORYload	0.2	0.298	1.699	0.593	0.839
	DISdiff	0.2	0.110	0.494	0.219	0.932
	MEMORYload + DISdiff	0.2	0.066	0.283	0.131	2.271
	MEMORYload ++ DISdiff +MEMORYload * DISdiff	0.2	0.023	0.096	0.046	9.452

Sup.Table 81 - Bayesian ANOVA results for the analysis of averaged alpha power (9:11Hz, 400:2000ms) (factors: MEMORYload, DISdiff) for the Right Motor region of interest.



IV. Discussion

GENERAL DISCUSSION

The research exposed in the present PhD thesis focuses on the interaction between selective attention and working memory. This interaction, although increasingly studied in the visual domain, has not been particularly explored in the auditory domain, especially during working memory encoding.

The first step was to create a new paradigm allowing to manipulate selective attention and working memory in an independent way. We used non-verbal auditory stimuli, which reduces the impact of language processing and allows future investigations in populations with potential language difficulties, in children for example. Thanks to pilot experiments, we were able to construct such a paradigm, that we called MEMAT for MEMory and ATtention. The first behavioral measures with control participants confirmed that we succeed in manipulating both memory and attention. Based on these results, we decided to go one step further and obtain more behavioral results, in order to 1) clarify new emerging hypotheses, and 2) test different categories of the population, with different attentional and memory profiles. Finally, we went a last step further and used this paradigm in combination with electrophysiological recordings, namely magnetoencephalography (MEG), in order to learn more about the interaction between selective attention and working memory at the level of the cerebral mechanisms.

Overall, the present research allows for 1) a better understanding of the interaction between selective attention and working memory during encoding 2) a better knowledge of inter-individual variability for attentional and memory capacities in the auditory modality, and 3) new findings on the brain mechanisms underlying auditory selective attention and working memory.

MEMAT PARADIGM CONSTRUCTION AND INTEREST

MEMAT is a paradigm combining a delayed-match-to-sample task and dichotic listening. If delayed comparison between two melodies composed of several tones can seem hard for non-musicians, it was proven to be manageable in several previous studies (Albouy et al., 2013; Dowling & Fujitani, 1971; Rong et al., 2011). We confirmed here that it can be performed even with a competing selective attention task during encoding.

Participants were less accurate under high versus low memory load, and for trials with hard-compared to easy-to-ignore distractors, confirming the manipulation of the task difficulties: it is harder to ignore irrelevant musical tones when they are closer in pitch to the relevant musical tones (Woods et al., 2001), and it is harder to spot smaller pitch differences in the absence of contour change (Caclin & Tillmann, 2018; Dowling, 1999; Dowling, 1978; Schulze et al., 2012; Schulze & Tillmann, 2013). Thanks to the lower-level perception task, we could confirm the individual ability to detect subtle tone changes, and therefore the absence of perceptual limitation for performance in the memory task. The perception task also allowed to isolate the effects of the distracting sounds from the memory load impact; as there is evidence for an absence of interaction between the distractor difficulty and the task on d' , the distractor impact is rather similar in both Perception and Memory tasks.

In MEMAT, balancing in terms of stimuli design and presentation was carefully thought out so that comparison between conditions could be made independently of the side of presentation of the stimuli, and without impact of the various generated melodies. This allowed us to use it in MEG without any major adaptation from the behavioral paradigm, the only necessity was to create more melodies to obtain more trials, which was simplified by the extension of the frequency range of the tones, and by previous automatized scripts for the melody generation. MEMAT in MEG was quite challenging for participants, as it was longer than the behavioral experiment, and it would have been too hard for them to include the perception task. In future experiments, as the difference between low and high working memory loads seemed hard to detect in MEG recordings, we could increase the difference between the two loads, or contrast one working memory task to a perception task.

MEMAT paradigm allowed us to investigate the interaction of selective attention and working memory, and in particular to show that these two processes share common cognitive resources.

A) Insights from behavioral results

The construction, data collection, and analysis related to the MEMAT paradigm has provided further knowledge on the interaction between working memory and selective attention. Behavioral results showed that the inhibition of all distracting sounds is hard when working memory is highly loaded (MEMAT-1, non-musicians, MHigh). For intermediary loads of working memory, there was a difference between easy- and hard-to-ignore distractors (MEMAT-1, non-musicians, MLow and MEMAT-1, musicians, MHigh). For a low load of working memory, there was no difference in performances between easy and hard to ignore distractors: they were all correctly inhibited (MEMAT-1, musicians, MLow).

Thanks to an adapted investigation in absence of distracting sounds, we showed that MEMAT task was easier to perform in the absence of distractors compared to the presence of easy-to-ignore distractors, including under high memory load. This underlines a strong distractor interference under high memory load and the requirement of cognitive treatment to inhibit distractors.

All these behavioral elements support the hypothesis of shared resources for selective attention and working memory. When both processes are under significant strain, they both appear to require a greater amount of cognitive resources, which limits their capabilities. The MEMAT experiment does not allow us to determine which one of the two processes could be prioritized over the other, *i.e.* which process would be best resourced. Indeed, as the task requiring an answer is that of working memory, filtering distractors is necessary to perform the task correctly.

Our results confirmed the partial overlap of attention and working memory in the visual domain. Indeed, performances in a working memory task were negatively impacted by concurrent distracting stimuli during encoding (Averbach & Coriell, 1961; Banks & Barber, 1977; Irwin & Zelinsky, 2002; Sperling, 1960). However, when performing an attentional task while encoding items in working memory, studies report no difference of attentional guidance abilities for different loads to encode (for a review, see Olivers, 2008), in contradiction with the present results showing that the higher the working memory load, the smaller the difference

between easy- and hard-to-ignore distractors. However, in most of the previous studies, participants have to memorize a new visual item for each trial, and then detect if in a target detection task, the new item searched being impacted by the presence of distractors that could have been the target in previous trials. Then, there might be a large amount of resources engaged in working memory and inaccessible for the attentional task, whatever the working memory load is (Soto et al., 2008; Woodman et al., 2007).

B) Insights from MEG results

The preliminary results extracted from MEG recordings during the MEMAT experiment allowed us to measure the impact of selective attention on transient and sustained evoked responses: for harder-to-ignore distractors, there was an increase of amplitude for the sustained responses and a decrease of amplitude for the N1 associated with the target, in keeping with previous studies (Bidet-Caulet et al., 2007; Fujiwara et al., 1998; Hansen & Hillyard, 1980; Hillyard et al., 1973; Kho et al., 2003; Näätänen & Picton, 1987; Neelon et al., 2006; Okita, 1979; Parasuraman et al., 1989; Picton & Hillyard, 1974).

Manipulating working memory load alone was found to impact transient (Albouy et al., 2013; Li et al., 2015) and sustained evoked responses (Albouy et al., 2013). However, we did not find yet any significant impact of working memory load neither on these responses nor on alpha oscillations power. In the work from Albouy and colleagues (Albouy et al., 2013), the working memory task was pretty similar to ours, but the difference of memory load was more important between conditions. Their results indicate an impact of the working memory load on the sustained response during the presentation of the S1. Further exploration will need to integrate a higher memory load difference, in order to try to detect an impact of working memory load on sustained sources. The presence of the dichotic listening task in MEMAT: 1) prevented us from separating the effects of distractors processing and targets processing in the sustained response, and 2) might have precluded to use a strategy of putting more resources during encoding for a more difficult memory task. In this case, effects of selective attention and working memory on brain processes would be separated in time, selective attention modulating sensory encoding, and working memory loads impacting the resources at stake during on-line comparison (during the S2 presentation). The balance between these two effects would then explain the interaction present in the behavioral results.

The absence of an impact of the working memory load on N1 to S1 might reveal that participants did not engage more resources in the encoding of the melody, even if they were aware of a higher difficulty to spot a difference in S2. This suggests that all their resources were used for attention filtering during the target and distractors presentation. MEG recordings during the perception task might be needed to test this hypothesis.

A tendency for an impact of working memory load on alpha oscillations power was noticed, but not significant in the analysis realized for now during the presentation of the S1. However, it was found in many research investigations that alpha is associated with demanding cognitive tasks, and that it increases during working memory maintenance (Leiberg et al., 2006; Sauseng et al., 2005; Sauseng et al., 2009). If processes share resources, they either modulate the activity in the same region, or are regulated by the same brain region: further explorations will allow us to decide in favor of one of these two hypotheses.

To our knowledge, there is no electrophysiological study on the interaction between working memory and selective attention during encoding. As an interaction between attention and memory is observed in behavioral results from the MEG experiment, one might expect to detect this interaction in further inquiries. In particular, further analyses should be performed to better understand this interaction at the brain level, such as investigations during the S2 presentation, gamma frequency analysis, or connectivity measures (see the section Perspectives, below).

We did not find a significant impact of the difficulty of the distractors on the alpha oscillations. However, the time-course and aspect of these alpha oscillations already provide information about the link between attention and alpha oscillations.

ATTENTION AND ALPHA OSCILLATIONS

Our MEG recordings allowed us to dissociate two sub-bands of alpha, low (7-9Hz) and high (10-12Hz) corresponding to a decrease in the auditory cortex and an increase in the visual cortex during the processing of auditory stimuli. This result is in line with previous findings in another attentional task (ElShafei et al., 2018). This could be a consequence of the existence of distinct independent alpha generators, specific to inhibition or activation of irrelevant or relevant sensory areas, that can be modulated by endogenous attention processes (Frey et al., 2014; Müller & Weisz, 2012; Weisz & Obleser, 2014).

Our results also show a desynchronization of high alpha in the occipital area during the presentation of the visual cue: all acts as if low alpha is associated with the auditory cortex, and high alpha with the visual cortex. This underlines that the dissociation between low and high alpha might not be related to the stimulation or inhibition of a brain area, but only depends on the brain area which is impacted. The measures of the alpha peak frequency also show that the prefrontal cortex seems to be modulated by the low alpha sub-band, whereas the motor cortex seems to be modulated by the high alpha sub-band.

Our results go in favor of a role of alpha oscillations in the contrast of processing between relevant and irrelevant probes, either facilitating the relevant stimuli, inhibiting the irrelevant ones, or both (Jensen & Mazaheri, 2010; Klimesch et al., 2007). However, recent studies tend to show that alpha oscillations would only facilitate, not inhibit sensory processing: alpha brain waves and steady-state visual evoked potentials have been tested via electroencephalography recordings, and alpha enhancement did not lead to the suppression of distractors processing (Antonov et al., 2020).

INTER-INDIVIDUAL VARIABILITY OF ATTENTION AND MEMORY ABILITIES

As the MEMAT paradigm relies on the use of musical stimuli, we started by testing non-musicians. But as musicians are known to have better working performances, their participation to the experiment was useful to study the impact of enhanced mnemonic capacities on the interaction between selective attention and working memory (see the first section of the results). In a mirroring approach, we also tested low and high frequency dream recallers, for whom the attentional profiles seemed different according to the literature.

We confirmed previous results of enhanced working memory performances for musicians compared to non-musicians. This enhancement had a great impact on the results. The musicians were less impacted by distractors, suggesting that their better working memory performances left more resources to selective attention processes. This result implies that their enhanced behavioral mnemonic abilities are not due to a more efficient and faster recruitment of many cognitive resources, but on the contrary to the necessity of less resources to perform equally or even better.

Studying low- and high-frequency dream recallers allowed us to show that these two categories of the population do have differences in terms of attentional processes. Our results underline that low-frequency dream recallers are associated with greater abilities to resist to hard-to-ignore distracting sounds, which is consistent with previous hints in diverse studies (Escera et al., 2003; Garcia-Garcia et al., 2008). If we consider this as a greater ability to inhibit distractors, then more resources might be eligible for working memory processes. However, this does not impact working memory performances, as there is no interaction between the factor group and the working memory load. Therefore, it seems that the impact of selective attention enhancement does not impact working memory and selective attention interaction as much as working memory enhancement does. This could mean that working memory processes require much more cognitive resources and energy than selective attention, for example.

Therefore, either low-frequency dream recallers use less resources for attention but this reduced requirement is not important enough to improve the working memory performances, or they use more resources, or use them in a better way, which precludes these resources to be allocated to working memory processes. These hypotheses will be explored thanks to the MEG recordings performed in these two participant groups.

PERSPECTIVES

Two main axes need to be developed regarding the present work: the completion of the analyses of the MEG data from 1) the whole group and 2) the comparison between low- and high-frequency dream recallers. Furthermore, MEMAT could be of great use in studying the development of the interaction between attention and memory during development in children (3).

A) MEG analyses – whole group

The main further analyses to be done concern MEG recordings. There seem to be an effect of memory load on alpha oscillation power during the encoding period, which has not been shown significant. However, the window of extraction and averaging of the alpha power used in statistical analyses might not be fully appropriate. In particular, the frequency of alpha low and high sub-bands appears to be quite different between subjects. The time window restricted to S1+DIS might not be appropriate as well: if we start to look for an impact of working memory load, then the entire trial can be taken into account, as participants were aware of the working memory load and might have consciously recruited more resources during the entire length of the trial.

Several parameters have also been put aside, as an inevitable consequence of time restrictions. Further prospects need to dig into the consequence of selective attention performance during encoding upon the other steps of working memory: during the delay period, and during the cue presentation. Finally, it is of great importance to analyze gamma power. Indeed, in the general introduction, we have already underlined how gamma activity is impacted by both working memory and attentional processes: gamma might be the place of interaction between these two processes, if there is such a place. Gamma power in the auditory cortex is enhanced for voluntarily attended in comparison with unattended auditory stimuli (Debener et al., 2003; Ray et al., 2008; Zaehle et al., 2009), and increase of gamma amplitude has also been associated with faster (Ahveninen et al., 2013) and better (Ahveninen et al., 2013; Kaiser et al., 2003) performance in target detection tasks. Gamma is also associated with visual working memory (O. Jensen et al., 2007; Kaiser et al., 2003; Tallon-Baudry et al., 1999), and is reduced in participants with music encoding problems in the right dorsolateral prefrontal cortex (Albouy

et al., 2013). Gamma oscillations could be the sign of higher auditory cortex activity allowing to process and encode musical stimuli.

B) MEG analyses – low versus high frequency dream recallers

Low- and high-frequency dream recallers have performed the MEMAT task while MEG signals were recorded. As their behavioral results exhibit group differences and selective attention differences according to the group, it will be of great interest to examine and compare their MEG data.

As we observed an impact of the difficulty of the distractors on transient and sustained responses, we expect these modulations to differ between the groups. Low-frequency dream recallers should exhibit greater difference of potentials between S1 and DIS. If the greater amplitude for the S1+hardDIS sustained response is due to a larger attentional process, we should expect differences between the groups at this level as well, but if it is due to a greater perceptual representation process, we might think that no group difference is to be expected.

C) MEMAT and cognitive development

Selective attention and working memory are two essential processes for learning, and understanding new concepts, things that children do most of their time. However, there are to our knowledge only very few investigations of the interaction between selective attention and working memory during childhood.

The adaptation of a paradigm from adults to children often induces major changes, due to the difference of cognitive abilities along childhood. The development of the cortical areas involved in working memory and selective attention processes continues until late adolescence, with major changes in voluntary attention and short-term memory from the age of 6 years (Dowling, 1999; Kanaka et al., 2008). The development of auditory memory in children aged 6-11 years is a poorly explored subject (Vogan et al., 2016), with in particular very few results on non-verbal memory.

As MEMAT does not rely on other particular knowledge such as language processing (which could be an obstacle for children), and as the only compulsory ability would be to be able to answer via a computer mouse or other responding click button, MEMAT seems very close to be appropriate for children starting from 6 years old, providing that the acoustical content of the stimuli is adapted to their perceptual abilities.

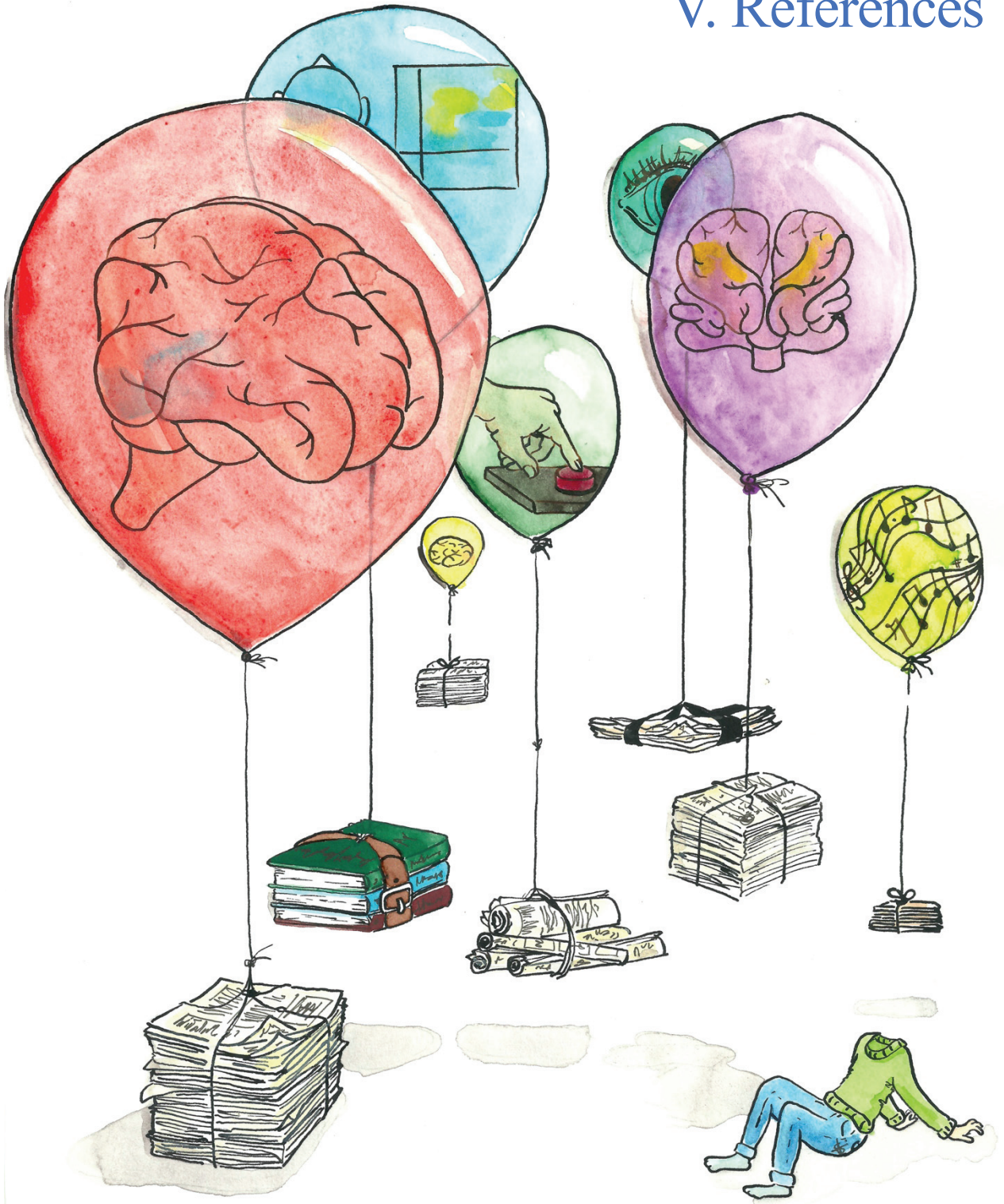
We might expect them to have poorer performances than adults, and to get better while growing up to 12 years old. Furthermore, if the task could be quite challenging for 6-year-old children, we might observe no impact of the difficulty of the distractors: all distractors would be too difficult to ignore. It might be necessary to add, as in MEMAT-2 (see Section 1 of the results) a condition without distracting sounds.

CONCLUSION

This thesis allowed investigating the interaction between non-verbal auditory selective attention and working memory processes. We designed a new paradigm able to test this interaction by manipulating these two processes in an independent way. Thanks to behavioral enquiries, we showed and refined how attention and memory can vary in the general population, and how this variation can impact cognitive interactions. Thanks to behavioral and MEG data, we showed that selective attention and working memory share cognitive resources, and that they seem to impact different brain mechanisms (respectively).

Further experiments and analyses need to be run using this new paradigm, in particular on acquired MEG data, but also on other categories of the population, such as children. It would also be of great interest to unify results from the visual and auditory modality, once the interactions at the brain level are clarified. In particular, understanding the interaction between selective attention and working memory for all modalities should help refining our environmental choices for the education of children and adults. For example, it can help them to reduce the number of irrelevant stimuli (in particular those most similar to the relevant stimuli) to filter them better, and therefore helping them to encode more precisely the relevant information.

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